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DISTRIBUTION AND MIGRATION OF THE REDHEAD

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Abstract: An analysis of the distribution and migration of the redhead (*Aythya americana*) was based on aerial survey and band recovery data accumulated by the U. S. Fish and Wildlife Service. Additional data from states outside routine survey areas were obtained from state waterfowl biologists and from published data. The redhead is prevalent in the prairie pothole region, predominantly in the south and west. The redhead has recently expanded to marginal range in Alaska and in several southern states, probably as a result of the serious drought of 1958-61. Approximately 78 percent of all redheads winter on the east coast of Texas in the highly saline Laguna Madre. About 14 percent use the East Coast (Chesapeake Bay to Florida), less than 3 percent the West Coast. Small numbers of birds will winter wherever water remains free of ice. Fall migration starts in mid-September and reaches its peak in mid-October. Most birds are on the wintering areas in late November and December. Birds from the south and west parts of the prairie region move due south to Texas; birds reared in the east and north sections tend to move to the East Coast. Most birds from the Great Basin area move due south or southeastward to winter in Texas; relatively few migrate to the East Coast. Movements are sufficiently distinct that breeding populations can be distinguished on the basis of the proportion of birds moving to each of the three major wintering areas. Banding of adults on wintering areas indicated that a small percentage of birds shift from one wintering area to another. Late summer northward and eastward movements are common among juveniles and adults. The present distribution and migration pattern indicates that the redhead originated in western or southwestern North America. It is suggested that the redhead has only recently invaded the prairie pothole region, either because of loss of habitat in its area of origin or because of the expansion of a successful species.

Knowledge of the geographic and ecological distribution of a game species is essential to an understanding of its biology and to the development of significant conservation practices. These data are especially valuable in the case of migratory species, such as waterfowl, which bear intense hunting pressure over a wide geographic area and are subject to severe habitat losses. Our knowledge of waterfowl distribution in North America exceeds that for any other continent and was made possible by both individual and organized programs aimed at the development of management techniques. To date, most published data are concerned with the delineation of breeding and wintering ranges and migratory pathways. However, survey procedures of the U. S. Fish and Wildlife Service have been directed toward collection of data on density of populations in various ecological zones. Brief summaries of these quantitative distribution data were prepared for the mallard (*Anas platyrhynchos*)

by Atwood (1957) and for the black duck (*Anas rubripes*) by Stewart (1958). Data on breeding and wintering ranges and migration of the canvasback (*Aythya valisineria*) were analyzed in detail by Stewart et al. (1958). The present paper summarizes similar data on the distribution of the redhead.

This summary is the result of the efforts of many individuals who recorded data on distribution, made intensive surveys, and banded redheads throughout North America. Noteworthy data were provided by the large number of bandings in California, Michigan, New York, and Utah. I am deeply indebted to these workers and to the many biologists who willingly furnished data on the status of the redhead in their locale. Earl Atwood, formerly of the U. S. Fish and Wildlife Service, originally encouraged my interest in this project and supplied much of the data. Walter Crissey, Robert Stewart, Dr. Aelred Geis, Charles Evans, and Allan DuVall of the U. S. Fish and Wildlife Service and Dr. Edward Riley of the New York State Museum offered suggestions and made data available to me. Many clerical workers at the Patuxent Bird Banding Laboratory assisted graciously. David Waller, Terry Jennings, Robert Locker, and Doris Weller assisted in the tabulation of data.

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DATA AND METHODS

The major waterfowl breeding area in the Dakotas and Prairie Provinces is surveyed twice annually by Flyway Biologists of the U. S. Fish and Wildlife Service. The spring survey of breeding populations (*population index* or *pair count*) and the summer production survey (*brood count*) provide data used to establish hunting regulations. These procedures have been summarized in detail by Stewart et al. (1958).

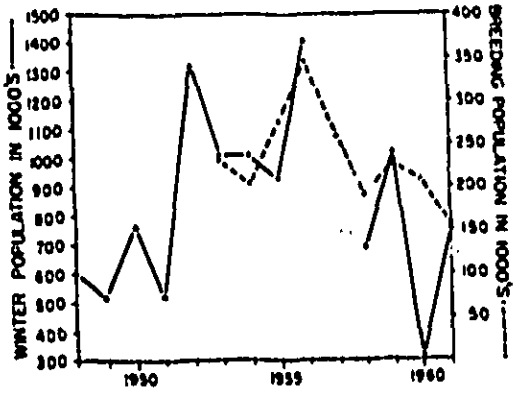

Fig. 1. Breeding and wintering populations of redheads, based on aerial survey data of the U. S. Bureau of Sport Fisheries and Wildlife. Winter data plotted for any given year are from the January preceding the breeding season.

Breeding population index figures for North America for 1953–61 are summarized in Fig. 1 with wintering population data. These data are from the annual waterfowl status reports (Crissey 1958, 1959, 1960, 1961) published by the U. S. Fish and Wildlife Service. A detailed analysis of population densities was made on data from the predrought period of 1951–55 for major breeding areas. An average index of birds seen per square mile surveyed was calculated (Table 1), and detailed examination was made of the 1955 data to establish accurately the geographic locations of populations within the sampling strata. Data for 1951–53 are not completely comparable with those of 1954 and 1955 because of slight modifications made during the development of techniques. However, these figures are of value in estimating density per unit area; more recent popula-

Table 1. Average population index figures and average number of birds per square mile in major areas sampled by the U. S. Fish and Wildlife Service, 1951–55.

Sample Area	Number of Years Sampled	Average Population Index	Average Number of Birds per Square Mile
Minnesota	3	3,005	0.01
Nebraska	2	6,540	0.42
South Dakota	5	21,221	0.42
North Dakota	5	35,858	0.76
Manitoba, Stratum A, southwestern (mixed prairie*)	5	51,005	0.99
Manitoba, Stratum B, west central (aspen parkland)	5	5,328	0.18
Manitoba, Stratum C, northern (parkland–coniferous forest ecotone)	5	042	0.01
Saskatchewan River Delta	5	3,871	0.98
Saskatchewan, Stratum A–E (aspen parkland)	4	6,548	0.38
Saskatchewan, Stratum A–W (mixed prairie)	4	22,033	0.00
Saskatchewan, Stratum B (aspen parkland)	4	30,593	0.00
Saskatchewan, Stratum C (shortgrass prairie)	1	4,113	0.37
Saskatchewan, Stratum E (coniferous forest)	4	2,803	0.02
Alberta, Stratum A (mixed prairie)	3	15,121	0.07
Alberta, Stratum B (aspen parkland)	3	21,051	0.87
Alberta, Stratum C (shortgrass prairie)	3	10,589	0.05
Alberta, Hay Lake Area	2	2,170	3.2
Alberta, Lake Athabasca Area	4	3,038	2.45

*General habitat type of sampling strata used in aerial surveys of the Prairie Provinces of Canada.

tion indices provide better data on total populations of large sampling units. The data presented probably overemphasize the importance of the Dakotas, since early survey techniques employed there involved circling potholes to obtain a more nearly complete count. Correction figures are not available.

The data presented are based on numbers of birds seen and have not been corrected in any way. Obviously, only a portion of the bird population is actually seen in any habitat even under the best conditions, and all data must be considered indices of abundance. Moreover, differences in habitat in various areas affect the visibility of birds to the aerial observer. Correction factors, devised by ground–air comparisons, are not yet reliable enough to be freely applied to data from all areas and for all species; nor are they available for all years during which surveys were made. In general, ground–air comparisons indicate that about 25 percent of redheads are counted on the breeding areas (W. F. Crissey, Personal communication).

In breeding areas where neither state nor Federal surveys were made, or where surveys were not comparable because of method or the small size of the area involved, notes on distribution and relative density were obtained from local biologists, the files of the U. S. Fish and Wildlife Service, and published literature.

Information on the distribution and size of wintering redhead populations was obtained from Fish and Wildlife Service annual midwinter inventory data (Table 2). State and Federal biologists made an intensive effort to census populations in early January when, presumably, most birds are on their wintering areas prior to northward migration. However, most observers agree (Crissey 1960) that the flocking behavior of redheads on the winter areas makes them extremely difficult to census accurately. Redheads flock in groups of tens of thousands (Jennings and Singleton 1953). Con-

Table 2. Total number of redheads observed during winter inventory of U. S. Fish and Wildlife Service, 1948-62.

Year	United States Flyways						Yearly Totals
	Atlantic	Mississippi	Central	Pacific	Canada	Mexico	
1962	98,100	10,351	315,631	8,405	210	12,857	475,550
1961	89,203	10,703	601,032	19,309	643	33,730	758,312
1960	39,180	9,110	188,373	8,361	1,384	61,547	310,907
1959	101,958	16,818	633,606	14,549	931	284,529	1,034,481
1958	127,152	33,950	107,088	6,785	311	108,000	683,492
1957	91,002	34,109	225,120	1,103	209	no survey	—
1956	158,611	15,191	1,085,577	21,721	501	124,130	1,407,001
1955	215,305	27,117	561,929	6,021	3,209	83,730	927,071
1954	119,395	8,953	822,470	4,013	2,279	125,709	1,083,419
1953	180,273	20,019	687,435	2,030	2,126	128,040	1,020,203
1952	181,140	7,132	1,051,113	5,877	2,110	89,752	1,337,721
1951	159,320	2,277	322,400	5,083	1,520	54,391	547,991
1950	116,182	5,135	591,375	2,670	4,251	32,831	753,741
1949	136,150	19,030	200,910	3,318	629	119,899	510,242
1948	52,250	7,201	283,113	3,712	6,000	241,072	597,378
Average	120,791	15,207	531,411	7,910	2,028	109,722	819,746
Percent	16	2	67	1	0.3	14	

siderable human error occurs when birds in such large concentrations are counted. Observers have made every effort to improve their accuracy by comparing sight estimates with data from aerial photographs (Singleton 1953), but high altitude photography must eventually be used to census these concentrations with a greater degree of accuracy. Moreover, flocks apparently shift from one area to another and even rest in salt water as many as 5 miles offshore (F. C. Wellein, Personal communication). These flocks are easily missed in a single survey, and the data indicate more severe yearly fluctuations than would be expected from variations in breeding success (Fig. 1) and hunting mortality. Nevertheless, these data do reflect the usual location and the approximate numbers of birds seen in a given geographic area and show gross trends of populations. When several surveys are made during the winter, more precise figures can be obtained.

Data on migration routes were obtained from plotting the geographic location of band recoveries of shot birds. These data are on file at the Bird Banding Laboratory of the Patuxent Research Center. All recoveries made prior to August 1, 1957, were examined, but only large samples of recoveries from birds banded as flightless juveniles (*locals*) or as adults on wintering areas or in spring migration were plotted on maps. Data from locals are highly informative because recoveries in the fall following banding provide the most precise record of lines of travel (Grissey 1955). Although few adults have been banded on breeding areas, some data on birds banded on postbreeding concentration areas are presented.

DISTRIBUTION OF BREEDING POPULATIONS

General Pattern of Distribution

Fig. 2. shows the breeding-ground distribution of the redhead. All known records of breeding of this species are noted, and data on the central prairie area (the largest enclosed area on the map), for which aerial survey data are available, are indicated by an index of birds per square mile. Other areas are merely circled. Nesting may be expected in any ecologically suitable water area between the known breeding areas marked on the map.

Ecologically, the redhead is a bird of

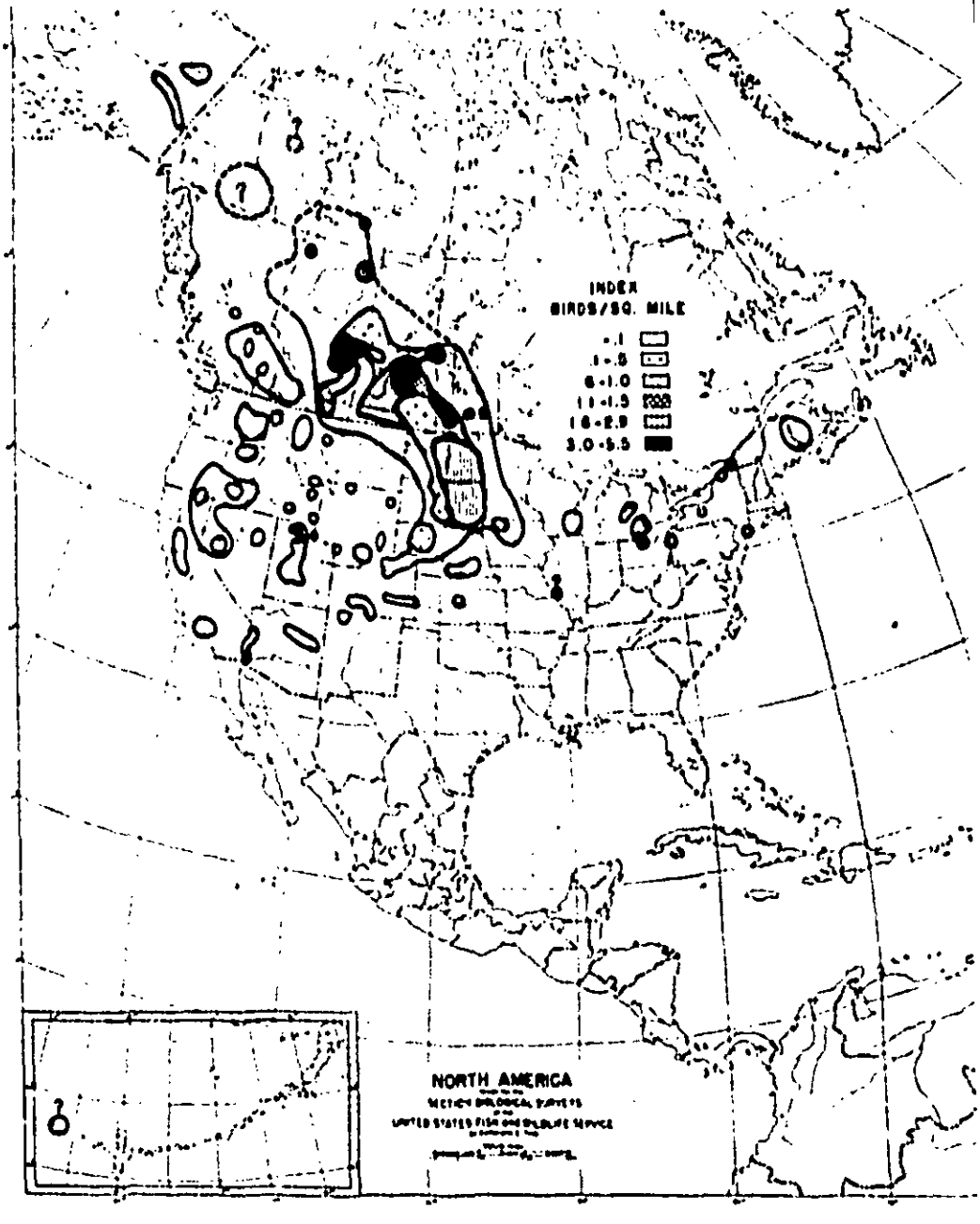

Fig. 2. Distribution of breeding redheads. Indicated densities in the large enclosed area in the prairie region are based upon aerial population-index data of the U. S. Fish and Wildlife Service. Dotted lines indicate inexact boundaries; question marks indicate questionable records or areas where birds are suspected of breeding.

unforested country with water areas sufficiently deep to provide permanent and fairly dense emergent vegetation for nesting cover. These requirements are met in the prairie pothole region of the Dakotas and the southern portions of the Prairie Provinces, in the semi-open aspen woodland lakes of central Manitoba, Saskatchewan, and Alberta, and in the alkaline lakes of the western United States. The major breeding area is the prairie–parkland region of central North America, where extensive lake areas accommodate the largest numbers of birds. Populations on limited lake areas in the West and on large marshes have much higher densities than are shown by most index figures but cannot be appraised in the same manner because of their small size. The gregarious nesting habits of the redhead in large western marshes were dramatically shown in the classic work of Williams and Marshall (1938) on the Bear River marshes of Utah. Other notable populations occur in the Malheur marshes of Oregon (Erickson 1948), the Tule Lake marsh in northern California (Miller and Collins, 1954), and in the Stillwater and Ruby Lake refuges in Nevada. Such areas are of much greater significance than their size indicates.

Obviously, distribution varies according to habitat factors, and the concentration of redheads in the prairie parkland of Saskatchewan may be a result of wet conditions in the southern part of the range and arid conditions in the west. The heart of the range probably undergoes little change.

In general, the redhead may be considered one of our most southerly species of ducks and one of the few common to the Southwest. The northernmost sizable populations are at Lake Athabasca and Hay Lake in northern Alberta. To the east, the range is limited by the coniferous forests of the Laurentian Shield, and no major populations occur east of Manitoba and western Minnesota. Coniferous forests also limit the distribution of the species in the intermontane region of British Columbia. The redhead is much less common on the Pacific slope and in the eastern deciduous forests.

Marginal Records and Isolated Populations

A detailed summary of records is presented here for areas which form the edge of the redhead's breeding range, where changes caused by climate and man are most severe. Western states with scattered populations also are included, but additional comments on the major central breeding area are deemed unnecessary. These records are arranged by geographic location in relation to the heart of the breeding range: northwest, northeast, midwest, and west.

Northwestern North America

ALASKA. There were no nesting records for the state until 1959–60, when several broods were seen and banded at lakes near Tetlin and Minto along the Tanana River and in the Fort Yukon area along the Yukon and Porcupine rivers (63–67° N latitude) (Hansen 1960, 1961). In 1959, several pairs were observed southwest of Anchorage and northeast of Kodiak Island (Hansen 1960). Prior to that, the redhead had appeared on Kodiak Island only as an accidental. Gabrielson and Lincoln (1959) questioned that and also noted that the Russians recorded the species on Saint Paul Island in the Pribilofs. A pair was observed by C. S. Williams (Personal communication) and O. J. Murie on May 11, 1948, on Amukta Island in the Aleutians. These workers also spoke with an Aleut chief on Attu Island who recognized the redhead from a painting and stated that redheads both nested and wintered in the area. The

chief called it by an Aleut name (Ka-vē-ine-much) meaning "round-head," which implies an ability to distinguish the redhead from the canvasback.

YUKON. Flyway Biologist Robert Smith reported (Personal communication) redheads common at 62–63° N latitude in the Northwest Territories, but he found no evidence of breeding. During 1961, Henry Hansen (Personal communication) reported sizable numbers of redheads in the southeastern Yukon (60–62° N), west of the Continental Divide. No brood survey was made but the large population index concurrent with the drought in the United States indicates potential breeders.

ALBERTA. Cooke (1906) was surprisingly accurate in estimating 51° N latitude as the northerly edge of the major redhead breeding range. However, the species is not uncommon at 55° in Saskatchewan and Alberta. A few isolated but dense populations exist in the Lake Claire–Lake Athabasca region (58° N) (Harper 1920, Jung 1930, Soper 1951) and at Hay Lake in northwestern Alberta (58° N). Preble (1908) reported a nest at Fort Resolution on the Great Slave Lake (61.5° N), but Seton (1908) made no mention of it.

Northeastern North America

MAINE. A pair of redheads was "evidently breeding," and a nest was found, near Calais in 1874 (Palmer 1949).

NEW BRUNSWICK. Mendall (1945) collected downy juvenile redheads and saw two females on the St. John River near Fredericton.

QUEBEC. Cayouette (1961) reported redheads nesting at Lac Saint Francois in Huntington County. Possibly these birds belonged to the released stock which now nests to the south at the Wilson Hill Game Management Area of the New York Conservation Department.

NEWFOUNDLAND. Bent (1923), noting that the redhead had been recorded as nesting at Sandy River, suspected a faulty identification. There appear to be no recent records to substantiate Bent's suggestion (Peters and Burleigh 1951).

NEW YORK. Benson et al. (1958) indicate that a brood was sighted at the Montezuma marshes about 1939; this record was not verified. Benson (Personal communication) also learned of similar reports in the early 1900's. No recent records for wild redheads are known, but hand-reared redheads were released at the Montezuma National Wildlife Refuge in 1952 and a few nestings have been recorded every year since the release. Similar success with hand-reared birds was recorded at the Howlands Island Game Farm marsh near Port Byron and at the Wilson Hill Game Management Area near Massena, New York.

Midwestern North America

PENNSYLVANIA. Nests and young were recorded and young were collected by Todd (1936) at Pymatuning Lake in western Pennsylvania. Apparently, breeding has occurred periodically, but the species has never been abundant.

OHIO. In addition to breeding at Pymatuning Lake on the Ohio–Pennsylvania border, the redhead has been reported occasionally in the Lake Erie marshes. In 1961, six pairs were found nesting at the Magee Marsh in Ottawa County (D. Handley, Personal communication). Presumably, this is a new breeding population.

MICHIGAN–ONTARIO. Several workers recorded breeding of the redhead at Lake St. Clair (Collins 1880, Baillie 1946, Lumsden 1951). In addition, two nests were found on Saginaw Bay of Lake Huron in 1941 (Baillie 1946). The first reported *inland* nestings in Michigan were in an artificial marsh near Saginaw (Kenaga 1954).

INDIANA–ILLINOIS. There appear to be no breeding records of redheads even though there are numerous lakes and marshes in northwestern Indiana and northeastern Illinois. Frank Bellrose, Illinois Natural History Survey, reported (Personal communication) that several surveys made in Illinois produced no evidence of nesting redheads. Sanford et al. (1903) indicated that the species possibly nested in Indiana, but Mumford (1951) found none and Edward Richardson (Personal communication) of Indiana has found no recent evidence.

WISCONSIN. There are several records of nesting in the lake region of southeastern *Wisconsin*. Goss (1891) reported a nest at Koshkonong Lake (Jefferson County), and several were reported in the Milwaukee area, near Green Bay in Door County, and at *Horicon Marsh in Dodge County*. Horicon Refuge manager, W. D. Carter, reported (Personal communication) that from 15 to 1,000 redheads have been produced on the refuge nearly every year *since* 1950. There was a generally higher population in the late than in the early 50's except for the peak year of 1954, when approximately 1,010 birds were produced.

MISSOURI. Whether the redhead ever nested in Missouri is questionable. There is a record in the files of the U. S. Fish and Wildlife Service for a nest found in 1937 at St. Albans near St. Louis. One of Cooke's (1888) observers in Kansas City, G. E. Stillwell, noted that the species "had bred." Widman (1907) made no mention of the redhead, however.

IOWA. Cooke (1888) reported that Clear Lake, Iowa (Cerro Gordo County), had the southernmost breeding record for the redhead, in his 1885 survey of the Mississippi Valley. Anderson (1907) reported the redhead as a *rare breeding bird* of northwestern Iowa. Tinker (1914) reported none in the area, but Bennett (1938) reported 30–40 pairs in Clay and Palo Alto counties during the 1930's. The species increased, and Low (1945) found about 90 pairs per year during 1939 and 1940. Their numbers declined gradually, and Glover (1956) noted about 25 pairs during 1948. Breeders were rare in the early 1950's but increased markedly in the late 1950's, following a drought. By 1960, the species was probably as common as during Low's (1945) study and was found from Dickinson and Clay counties eastward to Kossuth and Hancock counties (the lake country formed by the most recent glaciation).

KANSAS. Goss (1891) gave no indication that redheads nested in the state, but the species nested in the Cheyenne Bottoms area (Barton County) as early as 1925 (*Johnston* 1960). According to State Biologist D. C. Coleman (Personal communication), the species has been regular, though not abundant, in that area from 1957 to 1960, when *more* than 20 resident pairs were noted.

NEBRASKA. The redhead has been a common and regular breeding bird in the western Sandhill Lakes region (Oberholser and McAtee 1920). In addition, a population appears to have developed during 1960–61 in the South-Central Rainwater Basin area of Clay and Adams counties (George Schildman, Personal communication).

Western North America

COLORADO. The redhead occurs regularly, but not in large numbers. Hershey and Rockwell (1909) reported its nesting at Barr Lake near Denver (Adams County), and Bent (1923) said it nested in the San Luis Valley. The species still nests in the latter area, at the Monte Vista National Wildlife Refuge. M. G. Sheldon, U. S.

Fish and Wildlife Service, reports (Personal communication) that it also nests at Lake John in northwestern Colorado (Jackson County).

WYOMING. Redheads appear to be uncommon in Wyoming, presumably because of the scarcity of suitable water areas in the eastern grassland region. A few nest in the lake area northwest of Laramie (Albany County), northwest of Newcastle (Weston County), and near Lovell (Bighorn County) (G. F. Wrakestraw, Personal communication).

IDAHO. The species nests commonly at the Camas National Wildlife Refuge in southeastern Idaho and, according to McClanahan (1940), also nests at the Minidoka Refuge in south-central Idaho and in the lakes of extreme northwest Idaho.

MONTANA. The redhead is a common breeding bird in parts of Montana. The major concentration is in the potholes of the Nine Pipe and Pablo refuges south of Flathead Lake (Sanders and Flathead counties) (Dwight Stockstad, Personal communication). The species also is common at the Red Rock Lakes Refuge in southwestern Montana. East of the Continental Divide, Weydemeyer and Marsh (1936) reported it at Lake Bowdoin in Phillips County, where it [illegible] still nests in large numbers. It [illegible] at the Medicine Lake National Wildlife Refuge, and Ellig (1955) noted it at Greenfield (or Freezeout) Lake in Teton County.

NEW MEXICO. Wetmore (1920) reported redheads nesting at Lake Burford (also called Stinking Lake), Rio Arriba County, in 1918. Although Huey and Travis (1961) found resident birds to be common there and in other areas of northeastern New Mexico during 1959–61, they neither saw nor trapped young birds. William Huey, New Mexico Department of Game and Fish, reported (Personal communication) that approximately 10,000 redheads spent the summer on Wagon Mound Lake in Mora County in 1959. This was a dry year in more northerly breeding areas, and apparently these were nonbreeders. This group was absent in 1960 (a wetter year in the north), but smaller numbers again appeared in 1961, when the prairie drought was most severe.

ARIZONA. The redhead is an uncommon breeder in the state. A few nest on reservoirs of the Colorado River, on Mittry Lake near Yuma, and in lakes southeast of Flagstaff (Monson 1944, Fleming 1959).

NEVADA. Cooke (1906) reported the species common in the lakes of central Nevada. The two major areas are in the west and east-central part of the state. Victor Oglesby, Nevada Fish and Game Department, listed (Personal communication) the following breeding areas in order of importance: Stillwater Marsh (Churchill County), Ruby Lake (Elko County), Carson Lake (Churchill County), Franklin Lake (Elko County), Sunnyside Wildlife Management Area (near Sunnyside in Nye County), and the Humboldt Sink (Churchill County). Over 2,000 pairs nested on the Stillwater National Wildlife Refuge in 1959, and 652 pairs were recorded at the Ruby Lake National Wildlife Refuge during the same year (Crissey 1961). Such dense isolated populations are characteristic of the Great Basin, as shown by similar populations in Utah, northeastern California, and Oregon.

UTAH. The most outstanding concentrations of redheads reported anywhere are those of the Bear River marshes adjacent to the Great Salt Lake. These have been well studied and described by Wetmore (1921), Williams and Marshall (1938), and Wingfield and Low (1955). Sizable concentrations also occur at the Ogden Bay Refuge, and smaller populations are found

throughout the Great Basin portion of the state (Nolan Nelson, Personal communication).

CALIFORNIA. The major nesting area is at Tule Lake and Lower Klamath Lake in the Great Basin area of northeastern California, where several thousand pairs nest annually (Miller and Collins 1954, Grissey 1961). The species also nests in smaller numbers in the San Joaquin Valley but rarely in the Sacramento Valley, as apparently it formerly did (Elliot 1898, Dawson 1923). Cooke (1906) reported that it occasionally nested as far south as Los Angeles and Ventura counties, but there seem to be no recent records for this area and little habitat remains. However, the species apparently has nested at the Salton Sea National Wildlife Refuge, and several broods were recorded on the California–Arizona line at the Imperial Wildlife Refuge in Imperial County (Monson 1944).

OREGON. The redhead is the major species nesting at Malheur and Harney lakes in the Malheur Refuge in southeastern Oregon. This appears to be the only portion of the western range where both the canvasback and redhead nest in dense populations (Erickson 1948).

WASHINGTON. Yocum (1951) reported the redhead as the most common diver in eastern Washington. They are most common in the Columbia Plateau in east-central Washington (Yocum and Hansen 1960), with major numbers in Lincoln and Spokane counties and fewer birds in Douglas and Okanagan counties (R. G. Jeffrey, Personal communication).

BRITISH COLUMBIA. The redhead nests commonly, but not in large numbers, in the intermontane region. Records are available from the Okanagan Lake area (Munro and Cowan 1947) to Tachick Lake near Vanderhoof. A summary of biologists' records provided by R. D. Harris, Canadian Wildlife Service, indicates that the species breeds rarely in southeastern British Columbia (East Kootenay), occurs but is not common in the south-central Okanagan area, and is thinly scattered in the central Cariboo parkland and the southern Kamloops area. There are no nesting records for the Pacific slope or Vancouver Island. The species is most common around the Lac la Hache area which Cooke (1906) believed to be its northernmost nesting area in British Columbia.

Changes in Breeding Range Caused by Man

It is apparent that there has been little recent change in the boundaries of the redhead's breeding range. Although the species may have nested farther south in Minnesota, Iowa, and probably Nebraska, Colorado, and California, the area involved is minor. In general, populations in the west are scattered, and it is misleading to consider the total area of a western state as former breeding range because a few isolated populations are present. Figures based on such methods (McClanahan 1940, Martin et al. 1951) are not biologically sound.

The major recent reduction of range has been caused by the loss of water basins within a given area. This has been most severe in the eastern and southern portions of the range. In Iowa, for example, it was estimated that glacial marshes once exceeded one million acres. Less than 50,000 acres now remain (Mann 1955), mostly in state ownership. This area was undoubtedly top-caliber range continuous with the present good range of the Dakotas. Thus, range boundaries may change little while the nesting habitat decreases 95 percent. Losses of still greater magnitude have occurred in southern Minnesota, the Dakotas, and the Prairie Provinces of Canada, even though the remaining marshes

still support the most dense redhead population.

Responses of Breeding Populations to Drought

The breeding data presented in Fig. 1 are based on data from the heart of the range during normal to wet years, with plentiful water areas available. During the late 1950's and early 1960's, the major breeding area was hard-hit by severe drought, as bad or worse than that of the 1930's (Crissey 1958, 1959, 1960, 1961). Although we commonly consider diving ducks to be less venturesome than dabbling ducks (Hochbaum 1946), it is obvious that divers can shift populations under extreme conditions. Presumably, several years are required to make the shift; this is indicated by a comparison of the distribution of the population during the first years of severe drought (1958–59) with that of 1959–61, noting the increases in populations in other localities.

Several dramatic changes have been recorded: In Alaska, where the redhead had been reported only as an accidental, numerous birds appeared in the east-central part of the state in 1959, and several broods were recorded. In 1960 and 1961, several hundred adults and six or more broods were observed (Hansen 1961).

In northern Alberta and the Northwest Territories (MacKenzie District), populations increased nearly threefold from 1958 to 1959 and remained above average during 1960 and 1961 (Crissey 1961). Although Robert Smith (*in* Crissey 1961) pointed out that this increase had little significance for production, because of the small numbers involved, it does indicate northward shifting of populations.

The large numbers of redheads seen in the Yukon by Hansen (1961) suggest a similar shift. This area had not been formally surveyed prior to 1961, but casual observations showed no major populations at that latitude.

The increase in numbers of redheads in northern Saskatchewan and Manitoba was perhaps the most striking change and was of considerable significance to the total population. From 1954 to 1957, the index figures (in thousands) surged from 6, 10, 4, and 6, respectively, to 31 in 1960 (Table 3).

Water areas also were reduced in numbers and size because of drought in California, Idaho, Nebraska, Nevada, Montana, and Utah; but sizable increases in redhead populations were recorded in Utah and Montana, concurrent with the more extensive drought in the prairie pothole area. A similar increase occurred in the sandhill lakes of western Nebraska, where populations in 1961 were about 2½ times those of 1959. Even more significant was the apparently new population which developed in south-central Nebraska and showed a twofold increase from 1960 to 1961, even though water conditions were poor in both years.

In Ohio, where the redhead rarely nests, six pairs were noted at Magee Marsh in 1961. The species has a similar status in Kansas, where a sizable population appeared in the Cheyenne Bottoms Refuge.

In northern Iowa, the species returned to the Ruthven pothole area (Clay and Palo Alto counties), increasing from a few pairs in 1958 to over 60 pairs during 1960 and 1961. Moreover, the species spread to suitable marshes throughout north-central Iowa.

The availability of suitable water areas in the southern part of the range probably produced similar shifts in breeding populations during the drought of the 1930's: Sizable populations appeared in Iowa (Low 1945); in Pennsylvania, the species was recorded as a breeding bird for the first time,

Table 3. Breeding population indexes (in thousands) for Canada, 1954-62.*

Area	Year								
	1954	1955	1956	1957	1958	1959	1960	1961	1962
Northern Alberta and Northwest Territories	21	27	22	25	14	78	29	32	51
Southern Alberta	48	60	58	45	63	37	40	40	21
Southern Saskatchewan	73	85	153	112	59	41	47	26	22
Southern Manitoba	18	25	21	17	32	38	26	10	11
Northern Saskatchewan, Manitoba, and southern Ontario	6	10	4	6	0	0	31	22	11
Totals	169	207	258	205	168	214	173	130	122

* Prepared by Walter P. Crissey, U. S. Bureau of Sport Fisheries and Wildlife.

and unsubstantiated reports occurred in New York and Missouri. Although no intensive surveys were made in northern Canada during this period, Soper (1934) reported general agreement among residents that waterfowl populations increased considerably; and it was in 1936 that a pair of birds was reported in the Aleutians.

Such a response to changes in habitat is normal and is essential to the maintenance of a species common to areas where drought can be severe. But the redhead should not be considered as mobile as some dabbling ducks, nor infallibly capable of shifting locations until a suitable nesting place is found. Undoubtedly, much nonbreeding has resulted from adults returning home and finding their breeding areas dry (as shown in lesser scaup by Rogers 1959). And large populations of redheads south of the breeding grounds (such as these recorded in New Mexico) raise questions as to whether the birds fly north and then return south or do not return to the breeding area after an unsuccessful season. Those birds that do travel to their old nesting areas may be unsuccessful or may possibly engage in the aberrant parasitic laying common to the species (Weller 1959).

If birds are unsuccessful in nesting attempts, many must move elsewhere during later years, although we know nothing of this behavior. In general, young-of-the-year are known for wandering (Johnston 1961), but both young and adult redheads gain a wide geographic experience following rearing and breeding seasons (see below) and even adults must shift breeding areas under extreme conditions. Some trial and error is indicated by the arrival of late migrants in potential breeding areas, as noted in redheads, canvasbacks, and blue-winged teal in Alaska (Hansen 1961) and in dabbling ducks in Nebraska (Schildman, Personal communication).

Populations in Relation to Habitat

The breeding area of the redhead is centered in a vast group of glacial and river marshes. The area of greatest density is usually centrally located, although marginal areas may have very dense but isolated populations. These marginal populations may vary in size with habitat conditions in the core of the marsh belt.

After a series of years of *normal* rainfall, the central area is ideal, providing water areas of all sizes and with various amounts of cover. During *wet* years, many large marshes become open-water lakes, but, because many small areas become more suitable for divers, the area still holds much of its population. During *drier* years, the reverse is true—small areas are unsuitable for the species, but large permanent marshes become the major nesting areas.

Only during severe drought does the central pothole area become unsuitable and, at this time, marginal areas with water become vital (and, therefore, worthy of preservation). During the two major droughts of the 1900's (to date), rainfall has returned first to the southern part of the range; redheads have responded to these ideal marshes and utilized them until water levels reached a point of creating open water lakes. Because large areas are most often preserved in what is now marginal range, few small marshes are available to replace the better, large marshes which become suitable during high water. As a result, the population gradually shifts to areas having a greater variety of water types, which provides some suitable habitat in most years. Similar shifts probably occur when drought comes to the southwestern part of the range in Utah, Nevada, and California.

Although drought has its decimating effects, it also has long-term values. For after a wet period, the emergent vegetation essential for nests and brood cover is eliminated by floatation and by muskrats. Only after a severe drought will dense growths of emergents make possible a gradual trend toward ideal cover-water interspersion. This long-range cycle has been seen twice in the pothole area in northwest Iowa, where the redhead has been recorded as a rare breeding bird in some years and a common nester in others. Obviously, this massive natural *draw-down* is more severe today than in past years because of the influence of man on marginal production areas.

DISTRIBUTION OF WINTERING POPULATIONS

Winter inventory data from the pre-drought period of 1951–56 were averaged to determine the distribution of populations (Table 2 and Fig. 3). Known wintering areas are outlined, and percentages of the total are indicated where they exceed 1 percent. In order of importance, the major wintering areas are the Laguna Madre of Texas and Mexico (78 percent), Chesapeake Bay to Pamlico Sound (11.9 percent), Florida (4.5 percent—mainly the western part of the state), and the west coast of Mexico (2.3 percent). Only about 3 percent of the redhead population is scattered to more central and northerly areas.

Typical wintering areas are large bodies of water along the coast, well protected from heavy wave action. Although they often include water depths sufficient for shallow dives, this is not true of much of the Laguna Madre, where redheads often tip-up to feed. These large bays and lagoons are often brackish (for a description of the highly saline Laguna Madre, see Hedgpeth 1947), and, while free of emergent vegetation, are well supplied with submerged foods. Several observers have noted that redheads sometimes leave these bays and convene in the ocean several miles offshore. Whether these birds need fresh water is uncertain, but some workers have noted flights from brackish lagoons to inland freshwater lakes (Ferrell 1955).

Smaller populations winter inland wherever water remains open throughout the fall and early winter. In the central United States, water kept open by industrial use and pollution is used by redheads in Michigan (Hunt 1961) and other states. In the west, the mild maritime climate of the Pacific slope creates suitable open water at Flathead Lake in Montana and Okanagan Lake in British Columbia. A few birds also winter in Washington, Oregon, and northern California. Small groups occasionally winter in more rigorous climes.

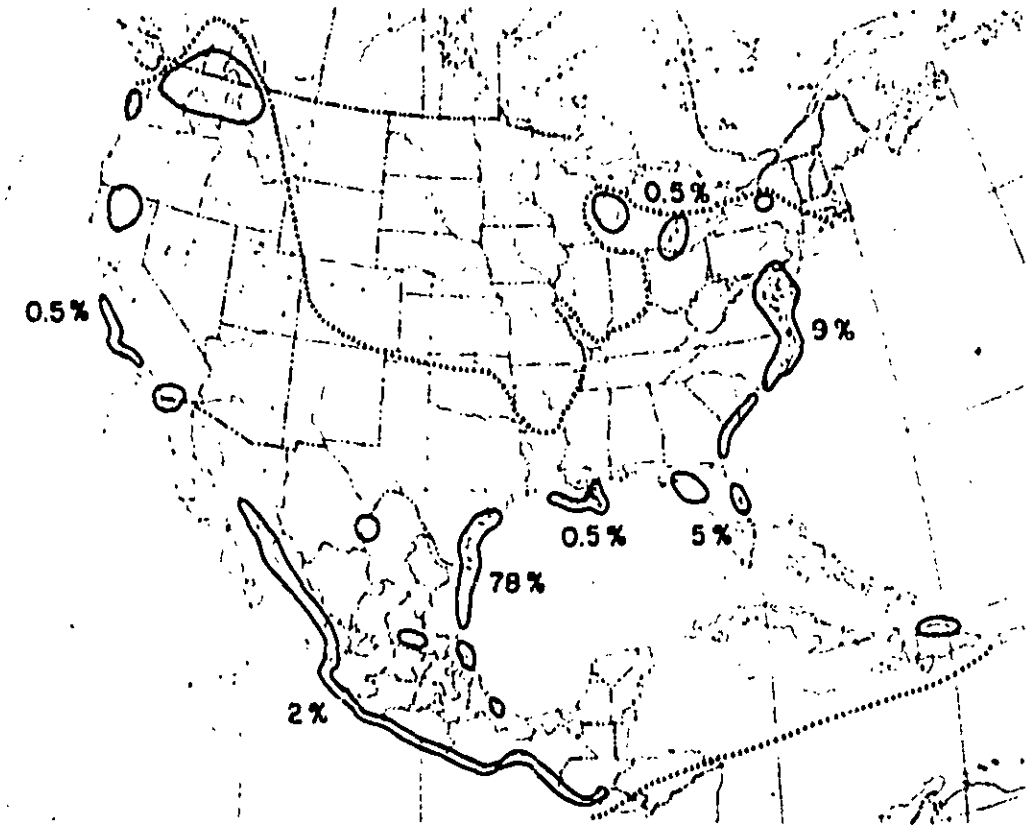

Fig. 3. Distribution of wintering redheads, based on winter inventory data of the U. S. Fish and Wildlife Service. Circled areas are known wintering grounds. The dotted line indicates the most northerly records for areas having 100 or more wintering redheads during 1951–55.

such as the Finger Lakes region of New York.

Relatively few redheads seem to winter in the interior lakes or in the valley of Mexico, where canvasbacks winter in sizable numbers. The redhead is not common south of Mexico. A few were observed in Guatemala during the winter inventory, and a few band recoveries were taken there. In 1953, 100 birds were recorded in the Dominican Republic. The species has also been recorded in the Bahamas, Cuba, Jamaica, and Bermuda (A.O.U. Check-list 1957).

Band recovery data may not give a precise indication of all wintering areas. Where redheads reach the favorable stopping areas during the shooting season, as in the Chesapeake Bay and Laguna Madre areas, recoveries are concentrated. Undoubtedly, however, some general southward shifting does occur after the shooting season. Thus, recoveries do not indicate any significant wintering in Florida or the Laguna Madre of Mexico, but winter surveys demonstrate that large numbers of redheads occur there during at least part of the winter. Recoveries seem to indicate that the Salton Sea is an important wintering area, but large concentrations of birds

are not found there regularly during early January.

FALL MIGRATION

All redhead band recoveries received during the predrought period prior to August 1, 1957, were plotted on individual maps according to banding station, sex, age, and time of recovery. Recoveries are plotted as *direct* (first fall and winter after banding) or *indirect* (later shooting seasons). Most emphasis was placed on recoveries of redheads banded as flightless juveniles (locals), because direct recoveries of these birds can be used to relate production areas to migration routes and wintering areas. There are many biases, however, and the reader is referred to Crissey's (1955) review of these problems. A most important factor to consider is that much movement of juveniles occurs in August and September, prior to the shooting seasons. Therefore, little of this movement is recorded by recoveries, nor are there sufficient banding stations to trap significant numbers of birds banded elsewhere.

Recoveries were analyzed from the standpoint of direction of travel toward one of the three major wintering areas; comments and figures are grouped according to areas from which birds move in similar patterns. No differential patterns according to sex were noted; therefore, the figures do not indicate the sex of each bird recovered. However, there was some differential kill of sexes according to geographic location. In the Laguna Madre and Chesapeake Bay wintering areas, the recovery ratio of adult males to females was 1.6 : 1.0 (391 : 242); recoveries of locals indicated a 1.4 : 1.0 ratio. On breeding and migration areas, however, adult males outnumbered females only 1.4 : 1.0, whereas female locals exceeded males in a 1.1 : 1.0 ratio.

Breeding Populations and Patterns of Movement

Breeding range can be divided on the basis of geography or ecology, but divisions are of major biological significance when they indicate populations differing in isolating behavior such as direction of movement and choice of the wintering area. Stewart et al. (1958) used movements of birds to wintering areas to divide the breeding range of the canvasbacks; the same technique was applied to band recovery data of redheads. Only direct (first fall) recoveries of birds banded as flightless young were used, and recoveries within the state or province of banding were not considered. One major problem which may have biased the calculations is the fact that recoveries from birds banded in the central plains area had to be in the extreme east or south before it could be assumed that they were heading toward the East or Gulf coasts. Thus, in estimating the ratio of dispersal to wintering areas, it was necessary to omit all recoveries from Canada, the Dakotas, Minnesota, and western Wisconsin. Based on direct fall recoveries, birds were considered to be moving to the West Coast wintering area if they were west of the Continental Divide, to the Gulf Coast if east of the Divide and west of the Mississippi, and to the East Coast if east of the Mississippi (Fig. 4). Numbers of recoveries from each of these three wintering areas are shown for each banding site (Fig. 4) from which 10 or more recoveries were available. Then, approximate boundaries were drawn to indicate zones having similar ratios of dispersal to each wintering area. Obviously, these boundaries are somewhat arbitrary and artificial and will be modified as further band recovery data become available. However, they do indicate a relatively clear-cut division of breeding populations.

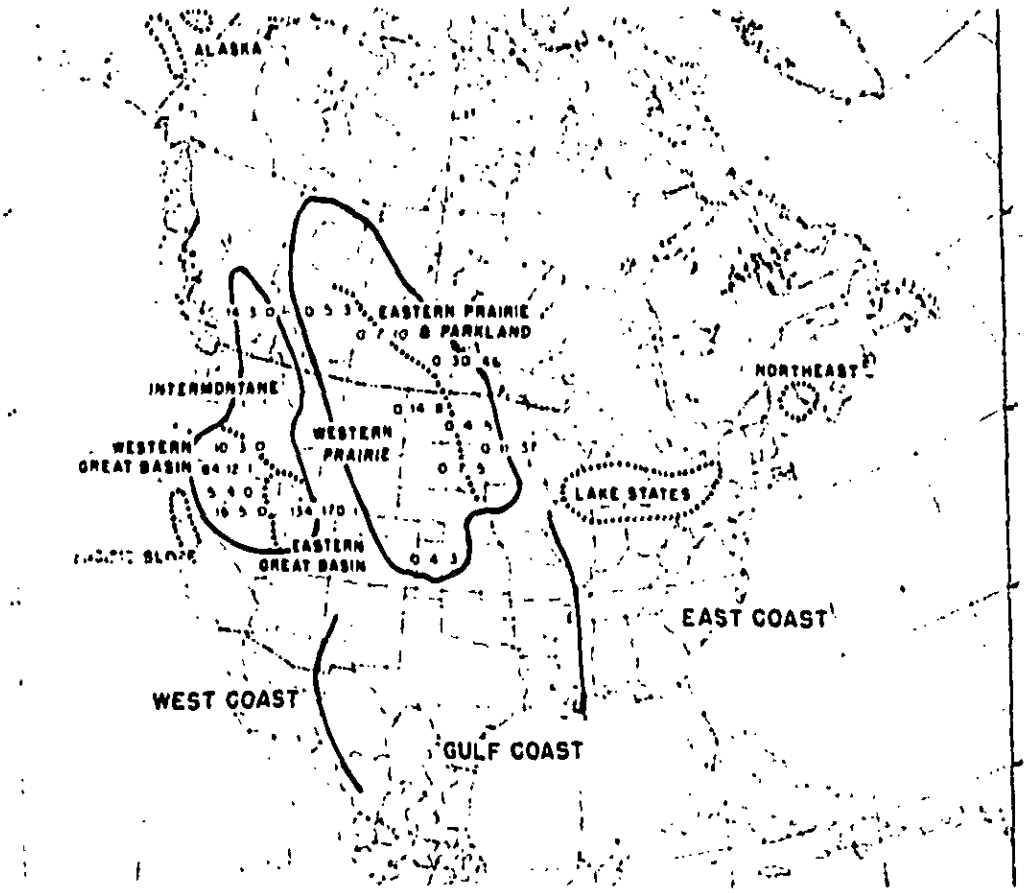

Fig. 4 Division of breeding range into regions and sub-regions, based on the dispersal of young to the three major wintering areas. *The ratios are the numbers of recoveries from bandings at the indicated sites, taken at or en route to* the West, Gulf, or East coasts.

helpful to the understanding of both the biology and management of the species.

Most birds reared in the glacial pothole area east of the Rocky Mountains (the prairie region) move to the Gulf or East Coast wintering areas. Birds reared in the west (Great Basin-intermontane region) winter on the West or Gulf Coast, with few birds moving eastward. At present, further subdivisions of these two major regions are tentative. The Great Basin-intermontane region may be divided along functional and topographic lines (Fig. 4). As expected, more birds from the eastern portion of this region move to the Gulf than to the West Coast. Because of the paucity of data for British Columbia, western Montana, and Washington, the separation of the intermontane subregion is based solely on topography.

The prairie region is more complex. In general, birds reared in the eastern portion of the region favor an eastward route to the Chesapeake Bay area, whereas more westerly birds move due south to Texas. There appears to be a gradual gradient

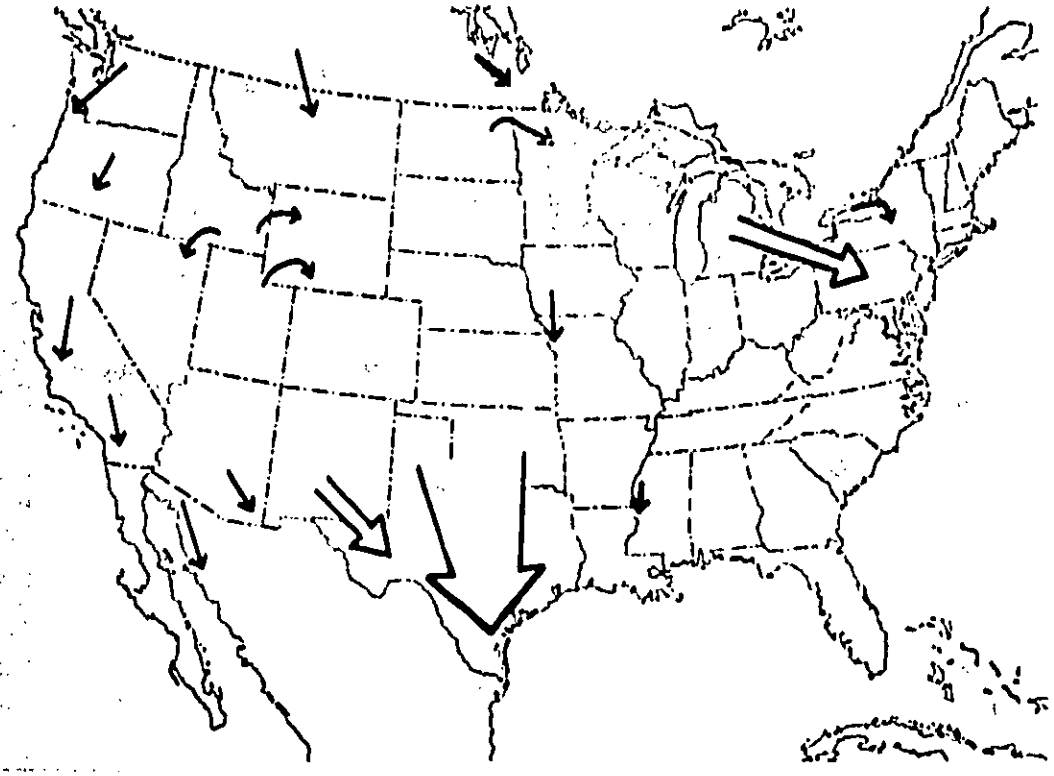

Fig. 5. Diagrammatic representation of the fall migration of the redhead. Width of the arrows indicates volume and is based on the percentage of birds using wintering areas.

from east to west. The dividing line depends on the boundaries used to separate routes to wintering areas. Whether a northern subdivision of this region should be made is uncertain, because of a lack of bandings in the north part, but most species which nest in the northern portions of the Prairie Provinces tend to move eastward.

Other breeding regions are named according to their geographic locations since insufficient data are available at present to determine the wintering areas these populations use.

Fig. 5 shows a general summary of the pattern of southward movement. The precise migration routes and the volume of birds moving over each route are not well known. The overland flight of large numbers of redheads in the south-central United States probably restricts the kill geographically and delineates only certain routes where water areas make shooting practical. The intense shooting pressure along the Great Lakes produces many band recoveries and, perhaps, depicts flight lines more clearly. Another bias in the figure is that we have no good measurement of the relative contribution of production on western breeding areas, which have dense but isolated populations. Nevertheless, Fig. 5 demonstrates a dramatic difference between the flight route of the majority of redheads and that of the canvasback, shown in Fig. 6 (adapted from data presented by Stewart et al. 1958). Al-

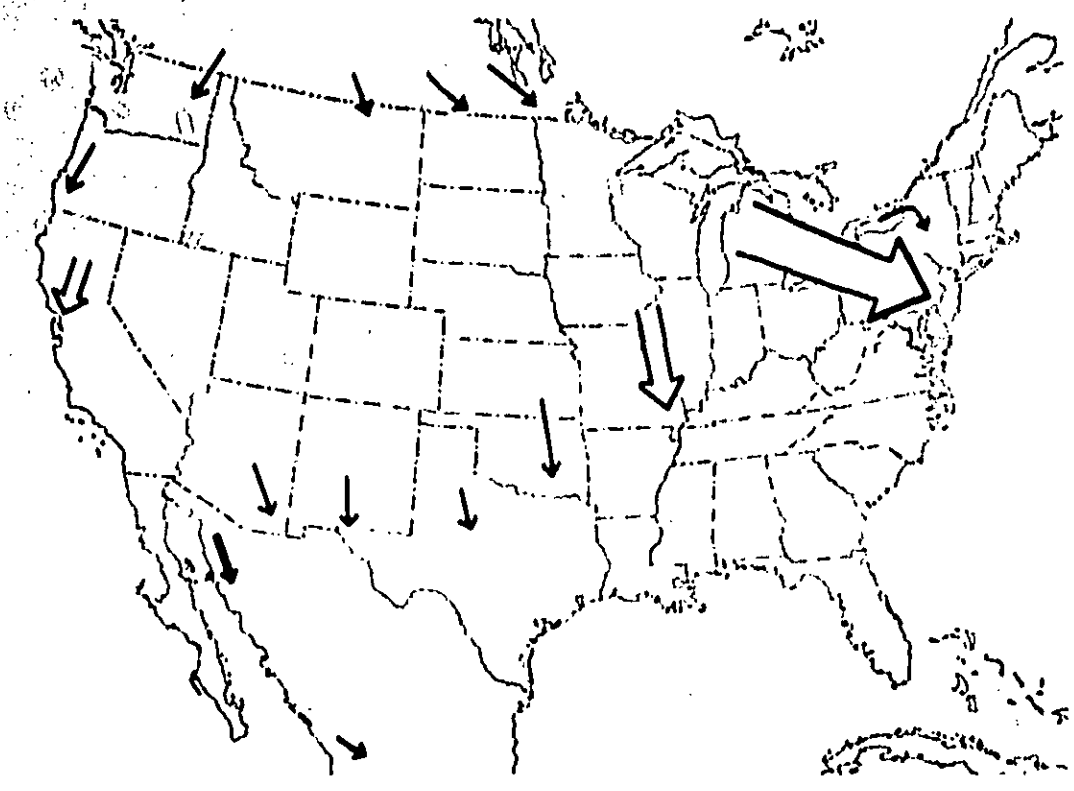

Fig. 6. Diagrammatic representation of the fall migration of the canvasback (after Stewart et al. 1958).

though the heart of the breeding range is the same for both species, their routes leaving this area are markedly different.

Regional Analysis of Movements of Locals

Prairie Region

ALBERTA. The limited bandings of locals demonstrate the similarity of movement of these birds to that of more eastern populations (Fig. 7). Only 2 of 11 direct distant recoveries (outside the banding state or province) was taken west of the Rocky Mountains. Recoveries are too few to have significance, but probably a slightly higher proportion of these birds move to Texas than to the East Coast. The three indirect recoveries were in the Central Flyway.

SASKATCHEWAN. Direct recoveries are about equally divided between flight lines to Texas and to the East Coast (Fig. 8). There were no recoveries to the west. *Indirect recoveries follow a similar pattern.*

MANITOBA. Redheads banded in central Manitoba appear to favor the Chesapeake Bay route, but numerous birds are recovered in Texas (*Fig. 9*). Several bands have been taken in Louisiana and several southeastern states, suggesting that the few wintering birds in this area originate in Manitoba. A few bands recovered from birds banded at Whitewater Lake in southwestern Manitoba indicate a slight tendency toward the Texas route and a pattern similar to that of birds reared in North Dakota. More northerly populations tend to move eastward, sending very few birds to the Texas wintering ground.

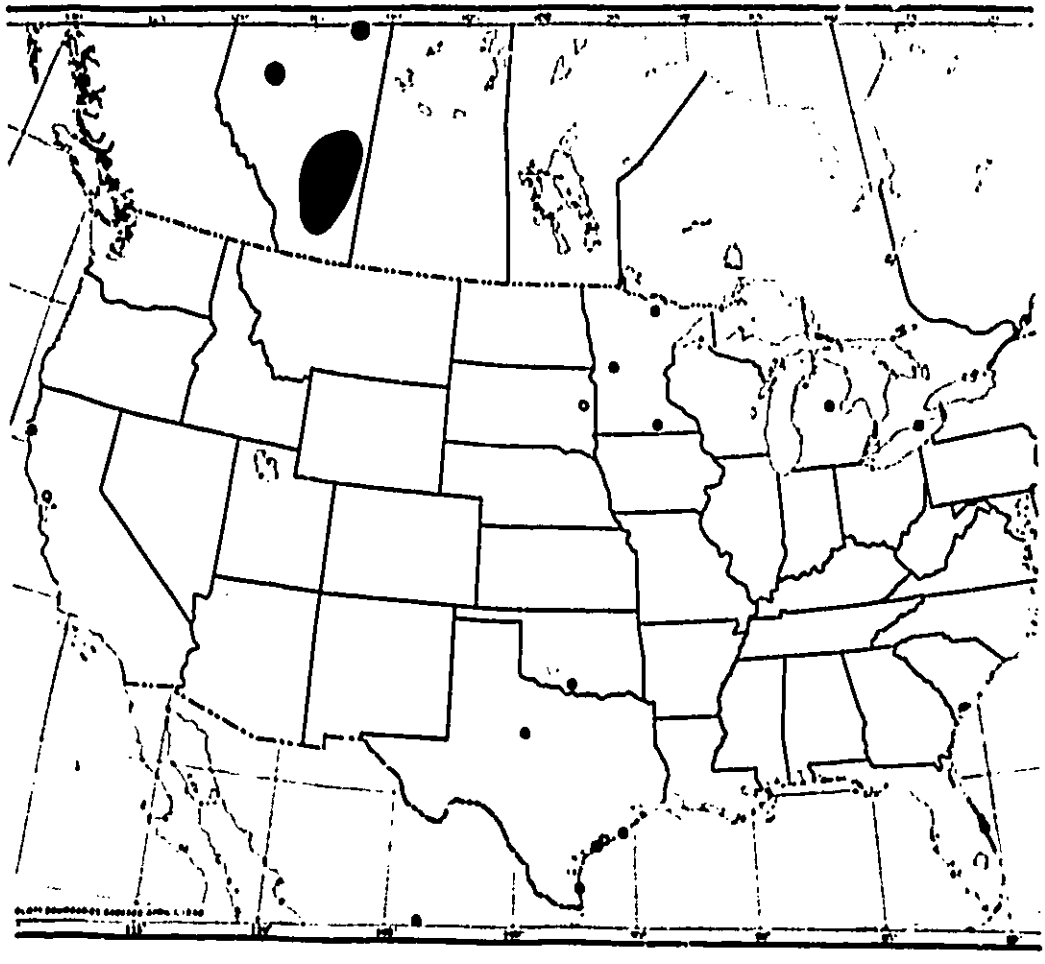

Fig. 7. Direct (dots) and indirect (circles) recoveries of *local* redheads banded in Alberta.

MINNESOTA. Birds from northwestern Minnesota (Mud and Tamarac lakes) move predominantly eastward, about twice as many recoveries coming from eastern states as from states to the south (Fig. 10). In this respect their pattern resembles that of birds from southern (but not southwestern) Manitoba.

An unusual pattern is suggested by banding recoveries in southwestern Minnesota. The six distant recoveries (direct and indirect) are all from the east. This may be chance, but some northward movement also is implied by direct recoveries from Manitoba.

NORTH DAKOTA. Locals banded in the western part of the state (Fig. 12) show a strong southerly movement due south to the Texas coast. Approximately twice as many recoveries were taken south as east. Few birds were taken in southeastern states. Birds banded in the eastern portion of the state show a pattern of movement similar to that of birds of eastern South Dakota (Fig. 11).

SOUTH DAKOTA. Banding in north-

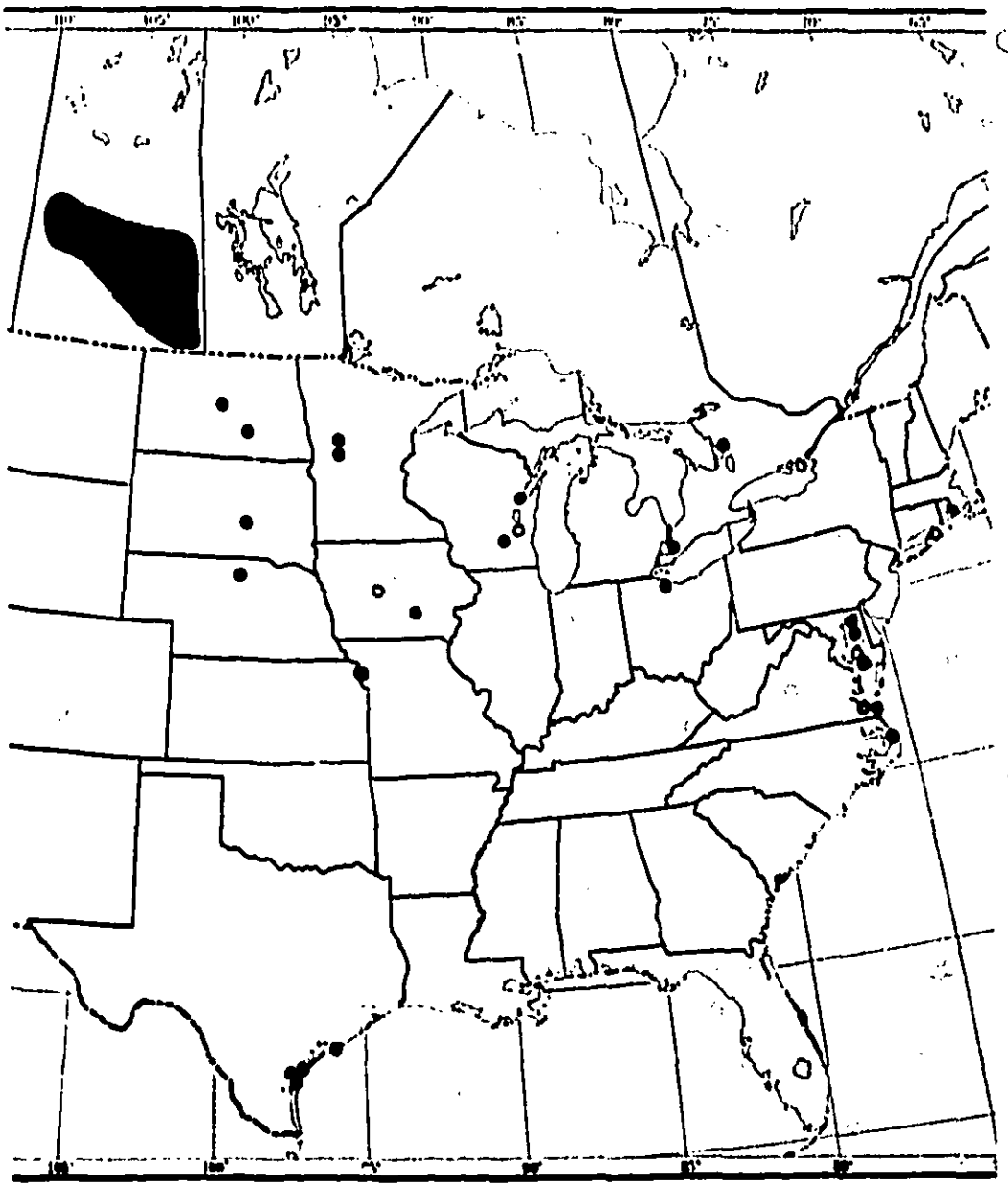

Fig. 8. Direct (dots) and indirect (circles) recoveries of *local* redheads banded in Saskatchewan.

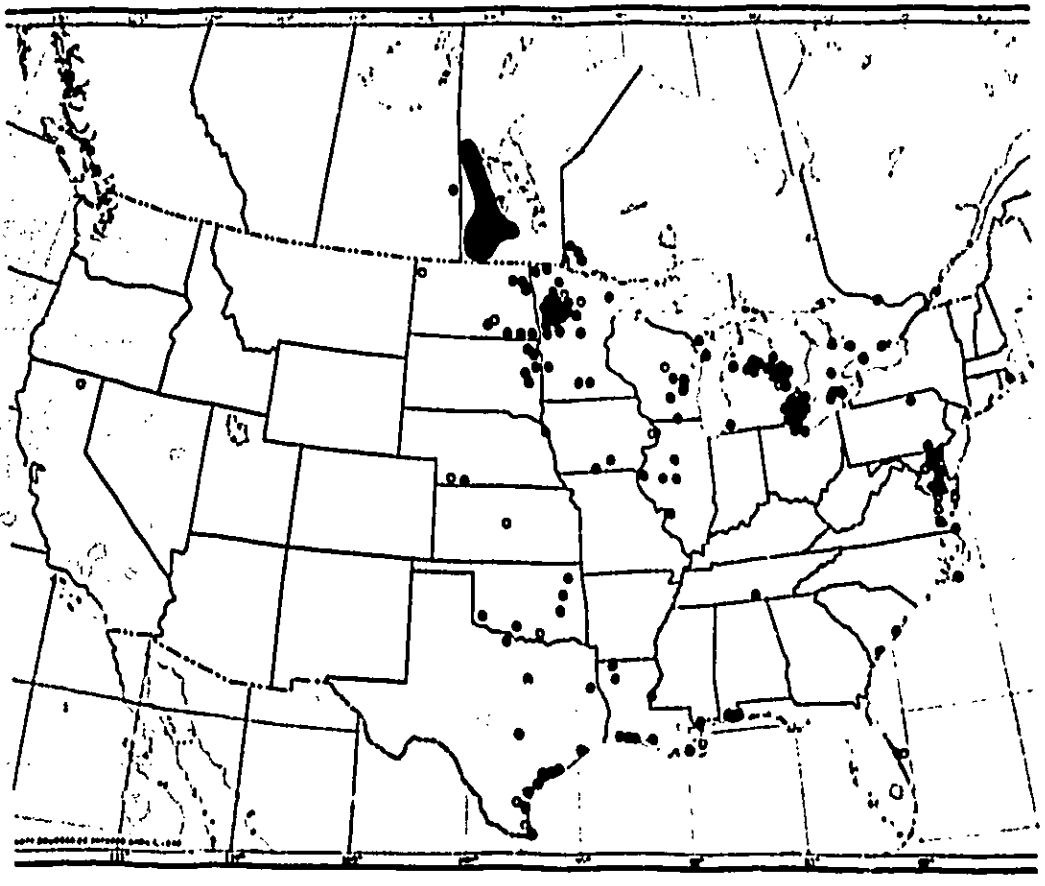

Fig. 9. Direct (dots) and indirect (circles) recoveries of local redheads banded in Manitoba.

eastern South Dakota has produced a limited number of recoveries showing a fairly equal division between south and east, with a few birds taken along the Mississippi River.

NEBRASKA. Recoveries show a surprising amount of northward and eastward movement, but an equal number of recoveries come from the south.

Great Basin–Intermontane Region

BRITISH COLUMBIA. Redheads reared in the northernmost portion of the intermontane region travel mostly due south toward the wintering area of southern California and the west coast of Mexico (Fig. 13). A few have been recovered in the Laguna Madre flight line. Hence, few cross the Rockies. Recent bandings of locals (1957–59) have produced 38 recoveries; several were east of the Rocky Mountains and in the Texas flight line. An interesting deviation is suggested by the indirect recoveries; six were east of the Rockies, two were west, and two were at the banding station.

OREGON. The distribution of the few recoveries of locals from Oregon bandings is similar to that of birds banded in British Columbia, California, and western Nevada (Fig. 14). Most of them travel due south.

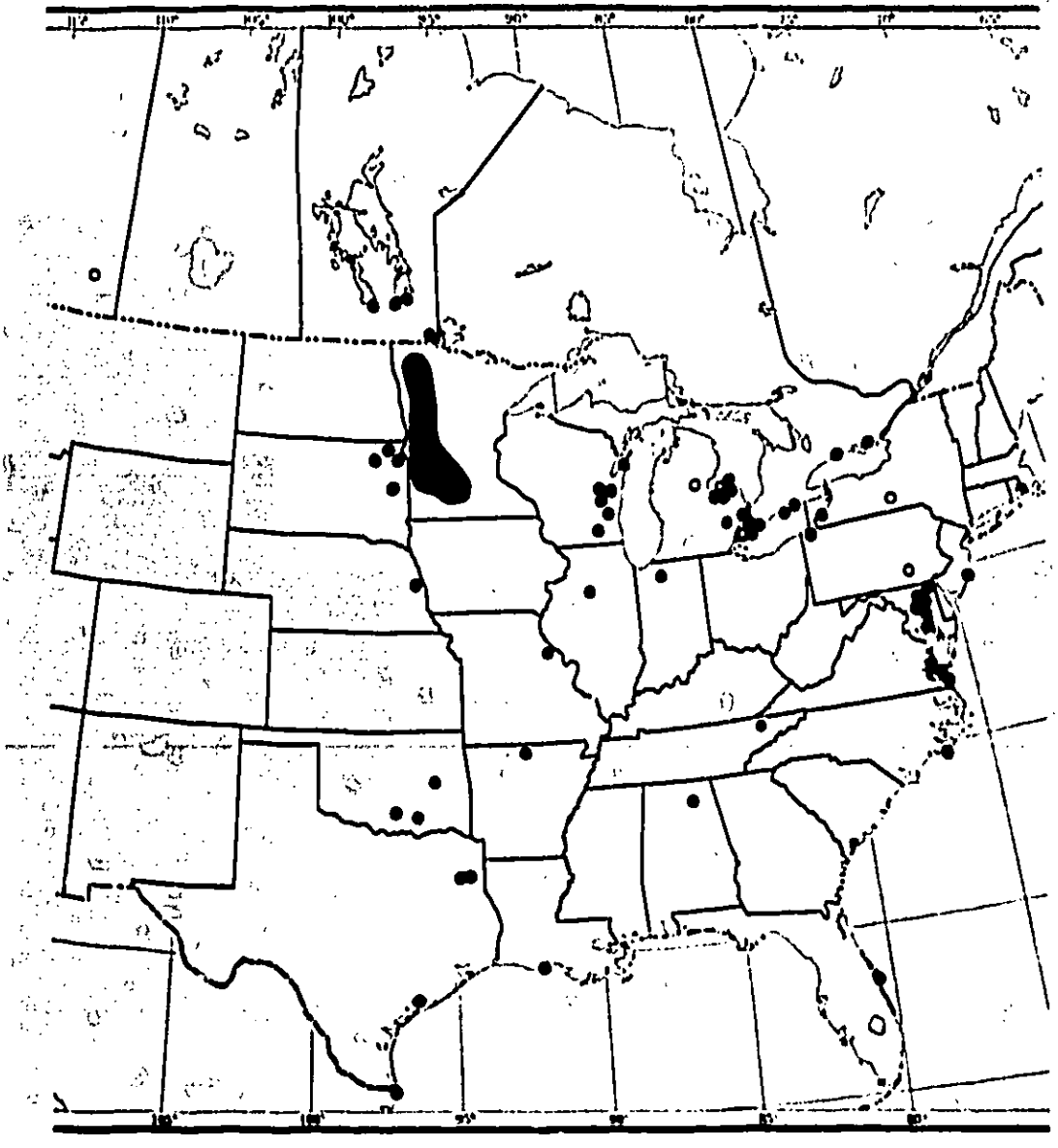

Fig. 10. Direct (dots) and indirect (circles) recoveries of local redheads banded in Minnesota.

but a few are taken in Utah and in eastern Texas. Presumably, Washington birds follow a similar pattern.

CALIFORNIA. Recoveries from bandings at Tule, Lower Klamath, and Honey lakes show a similar pattern of distribution so like those of Oregon and Nevada that they are plotted together (Fig. 14). Most birds from this area travel due south to winter in southern California and western Mexico. A few are recovered at Bear River in Utah and in the flight line toward, and

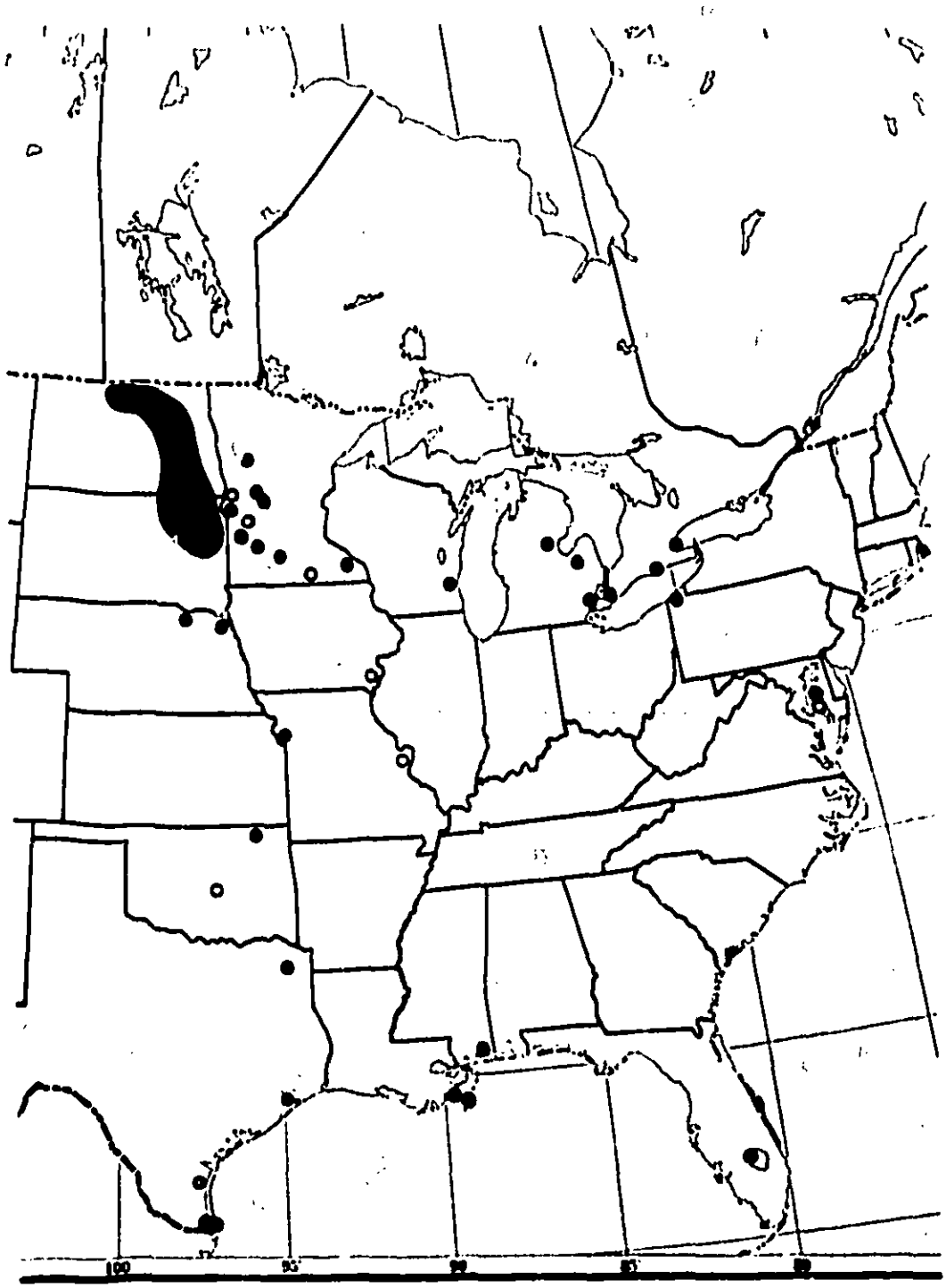

Fig. 11. Direct (dots) and indirect (circles) recoveries of local redheads banded in eastern North and South Dakota.

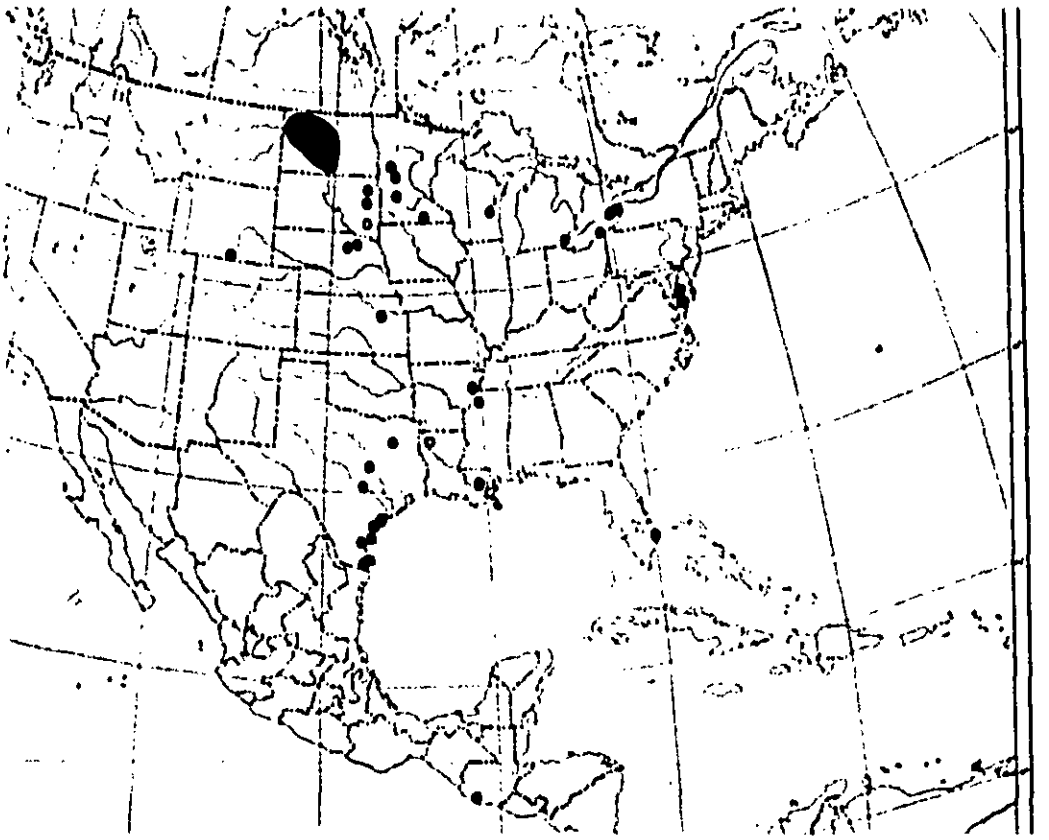

Fig. 12. Direct (dots) and indirect (circles) recoveries of local redheads banded in western North Dakota.

at, the Laguna Madre. One direct recovery was made in the Currituck Sound area. Of special interest is the northward movement demonstrated by direct recoveries in northern Washington and Idaho. As noted for bandings in British Columbia, a significantly higher number of indirect recoveries come from the more easterly areas than is true of direct recoveries.

NEVADA. Bandings at the Stillwater National Wildlife Refuge show a recovery pattern similar to that of California and Oregon (Fig. 14), but with some of the characteristics of the pattern noted in the Utah population. Six of 24 direct distant recoveries show eastern movement into the Central Flyway. Like nearly all other areas in this region, numerous indirect recoveries are taken east of the Rockies, and one was recorded in central Saskatchewan.

UTAH. The dense redhead population in the Bear River and other extensive marshes in the Great Salt Lake area is both complex and unique. It has been a major breeding area, and large numbers of flightless young have been banded there. It was the site of the earliest major banding effort (Wetmore 1923, Lincoln 1934, Van Den Akker and Wilson 1949), and later bandings produced recoveries leading to the first sound appraisal of the migration and mortality of any duck species (Williams

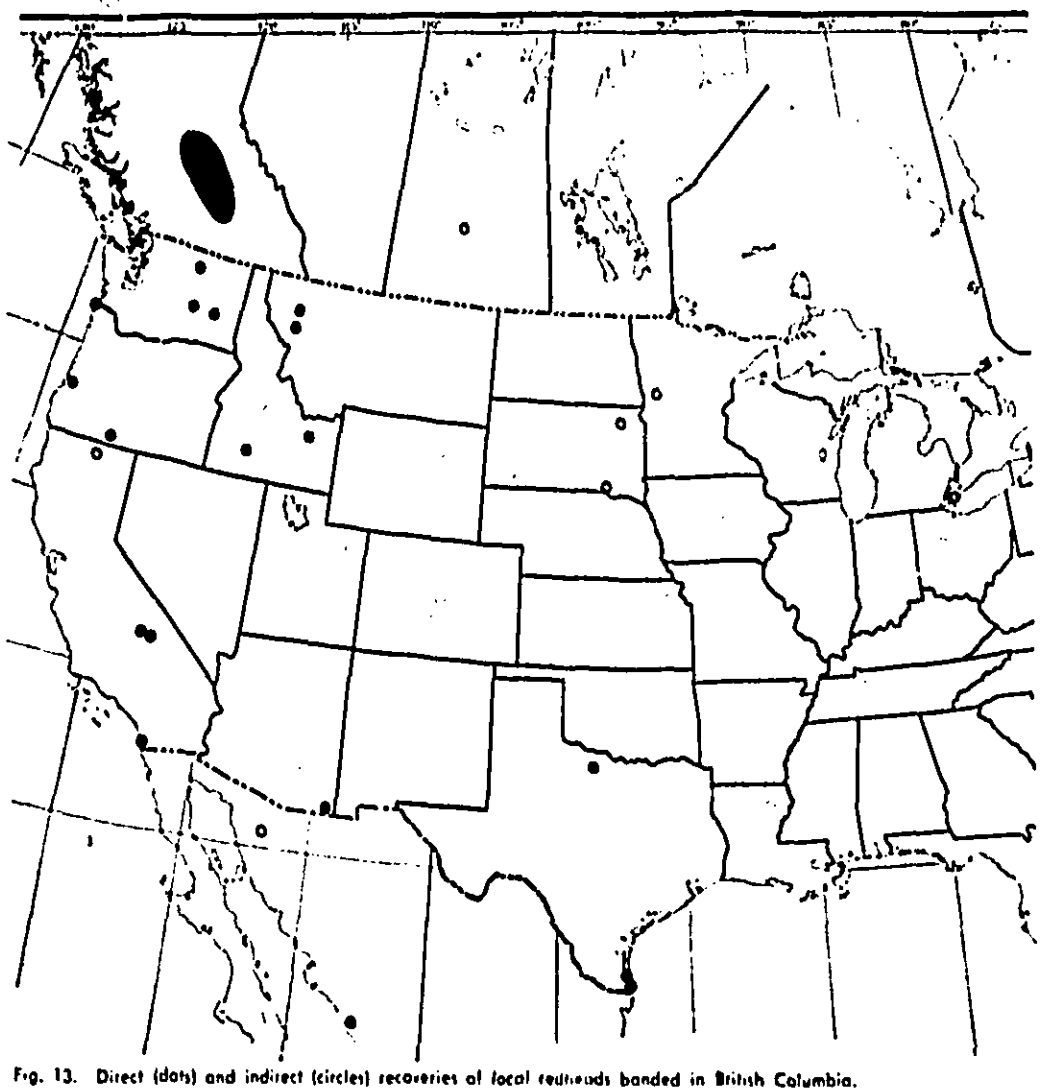

Fig. 13. Direct (dots) and indirect (circles) recoveries of local redheads banded in British Columbia.

1944). Williams' summary on migration of redheads from this area is still excellent, and more recent banding upholds his conclusions.

Because of the volume of recoveries from birds banded in the Bear River marshes, direct and indirect recoveries are plotted on separate maps. Direct recoveries are plotted on two maps to show pre- (Fig. 15) and post-1940 (Fig. 16) recoveries. After 1940, shooting pressure intensified (probably in Mexico as well as the United States), and shooting seasons started later in the fall (usually mid-October instead of mid-September). These figures indicate a significant decrease in the kill of redheads in the northern states. Wyoming and Montana show strikingly fewer recoveries since 1940. The apparent increase in kill in Mexico may indicate increased reporting

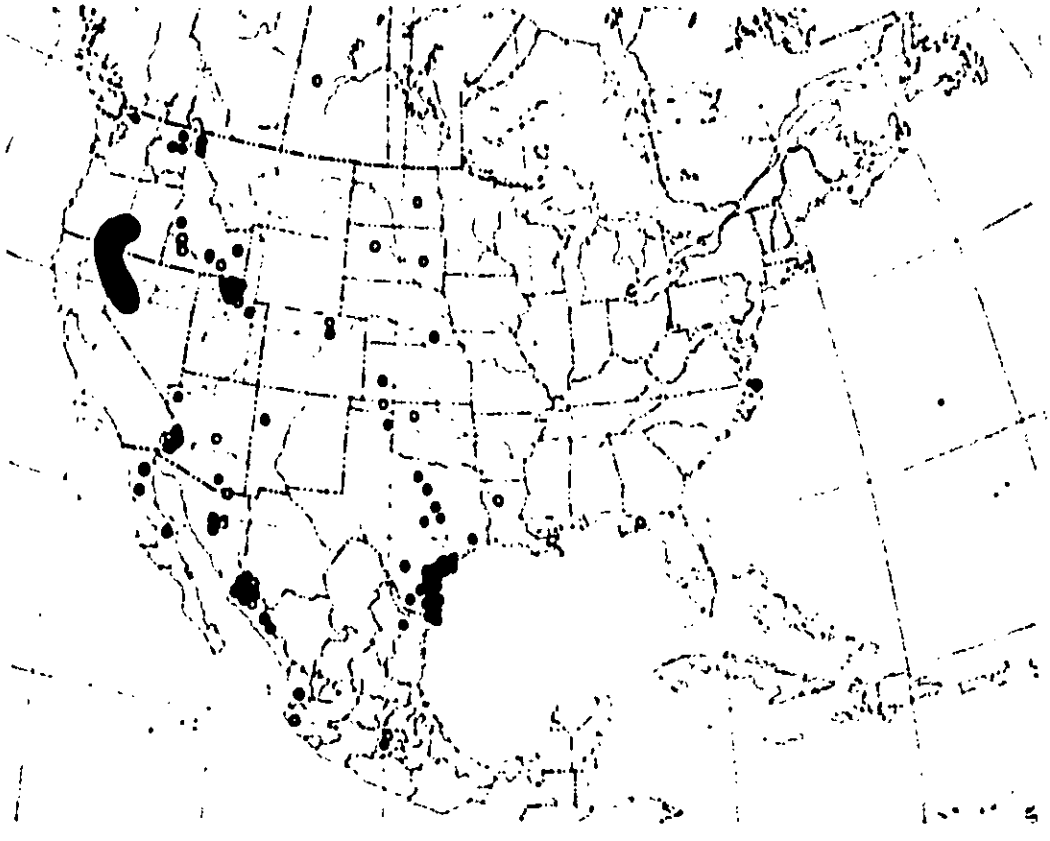

Fig. 14. Direct (dot) and indirect (circles) recoveries of *local* redheads banded in southeastern Oregon, northeastern California, and northwestern Nevada.

of bands, caused by American hunters or educational programs.

Most Bear River redheads move eastward through Wyoming and Colorado, and south to the Laguna Madre of Texas (Figs. 15–17). A lesser, but sizable, number move westward and are recovered in Nevada, California, and western Mexico. As with other Great Basin populations, direct recoveries are rare east of 95° longitude. A significant northward movement is indicated by direct recoveries (Figs. 15 and 16).

Indirect recoveries of birds banded as locals demonstrate a strong northward and eastward movement (Fig. 17). Such records could come from (1) birds that moved north after attaining flight and returned to that area to breed; (2) yearlings that nested at Bear River, flew northward in late summer, and thus were killed while going due south; or (3) birds that moved due north, with birds from Texas, and never *homed* to the rearing area. In any case, birds that summer in the far north probably join the eastern flight routes and continue eastward, some even going to Chesapeake Bay. Males are more common in these records than females, although both are present in the Dakotas. Only 16 indirect recoveries of both sexes have been reported in the Bear River area, suggesting

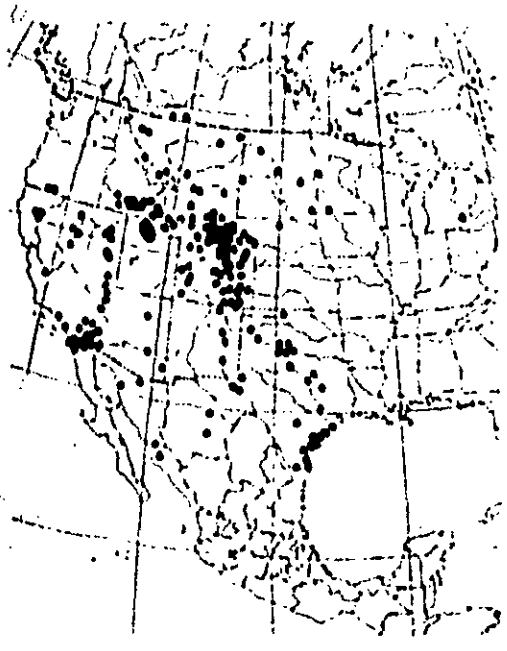

Fig. 15. Direct recoveries of local redheads banded in the Bear River Marshes of Utah prior to 1941.

that few birds remain in the area after breeding.

Adults Banded During Summer and Fall

There has been relatively little banding of adult redheads, but samples from southern Manitoba, North Dakota, and Oregon merit presentation (Figs. 18 and 19). These bandings were made from July to October, and, in most cases, there is no way of knowing whether these birds nested in the area of banding or were in postnesting concentrations. However, they do provide information on movement of adults from the same geographic areas where locals were banded.

In general, both direct and indirect recoveries of adults banded in fall suggest a pattern of southward movement similar to that of juveniles banded in the same area. As with locals, direct recoveries from areas north of the banding site have been noted from bandings of adults in California, Utah, Nevada, North Dakota, Saskatchewan, and Manitoba.

Fig. 16. Direct recoveries of local redheads banded in the Bear River Marshes of Utah since 1940.

Although very few redheads have been banded during June (when, presumably, they would be on breeding areas), recoveries from June bandings in Manitoba and Saskatchewan show a migration pattern

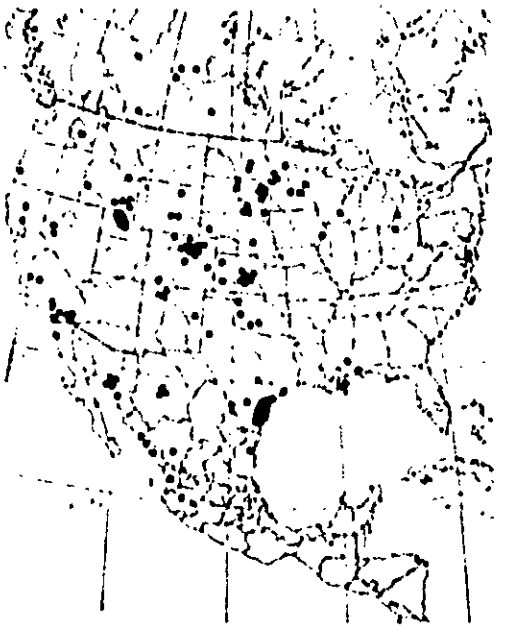

Fig. 17. Indirect recoveries of local redheads banded in the Bear River Marshes of Utah.

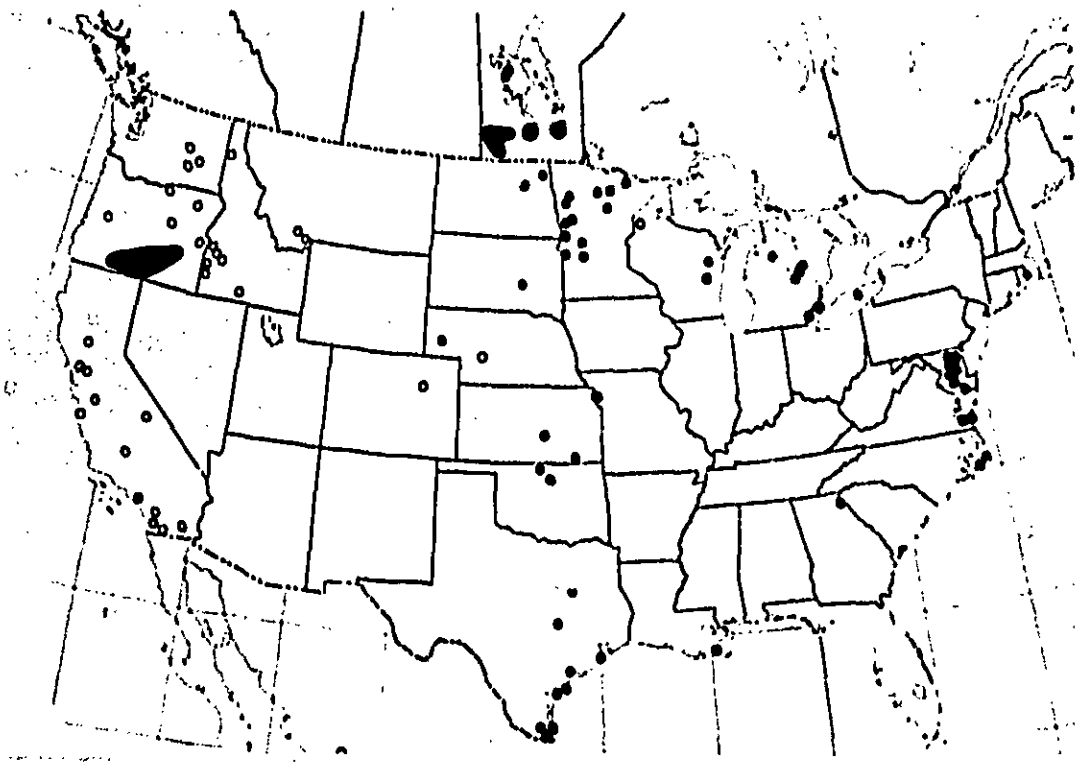

Fig. 18. Direct recoveries of adult redheads banded in southeastern Oregon (circles) and in southern Manitoba (dots).

similar to that of birds banded later in summer.

Adults Banded During Winter and Spring

Birds banded on wintering areas and in spring migration are considered adult even though yearlings are less than 1 year old. These birds have all engaged in at least one southward migration and become familiar with one wintering area. Most bandings of this type have been done in the eastern flight line in Maryland, New York, and Michigan, and in the Texas flight line in Oklahoma, Kansas, and Nebraska. Bandings in these areas can clearly be associated with one wintering area whereas those in the Dakotas or Minnesota must be considered separately, to avoid problems resulting from banding of mixed populations.

Figs. 20–23 demonstrate that birds banded in either flight line *tend* to return to the same wintering area via the same

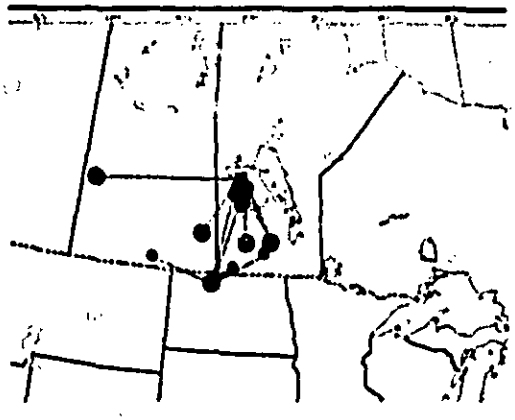

Fig. 19. Direct fall recoveries of adult redheads banded *during the postbreeding season in southern* Saskatchewan and Manitoba and in northern North Dakota.

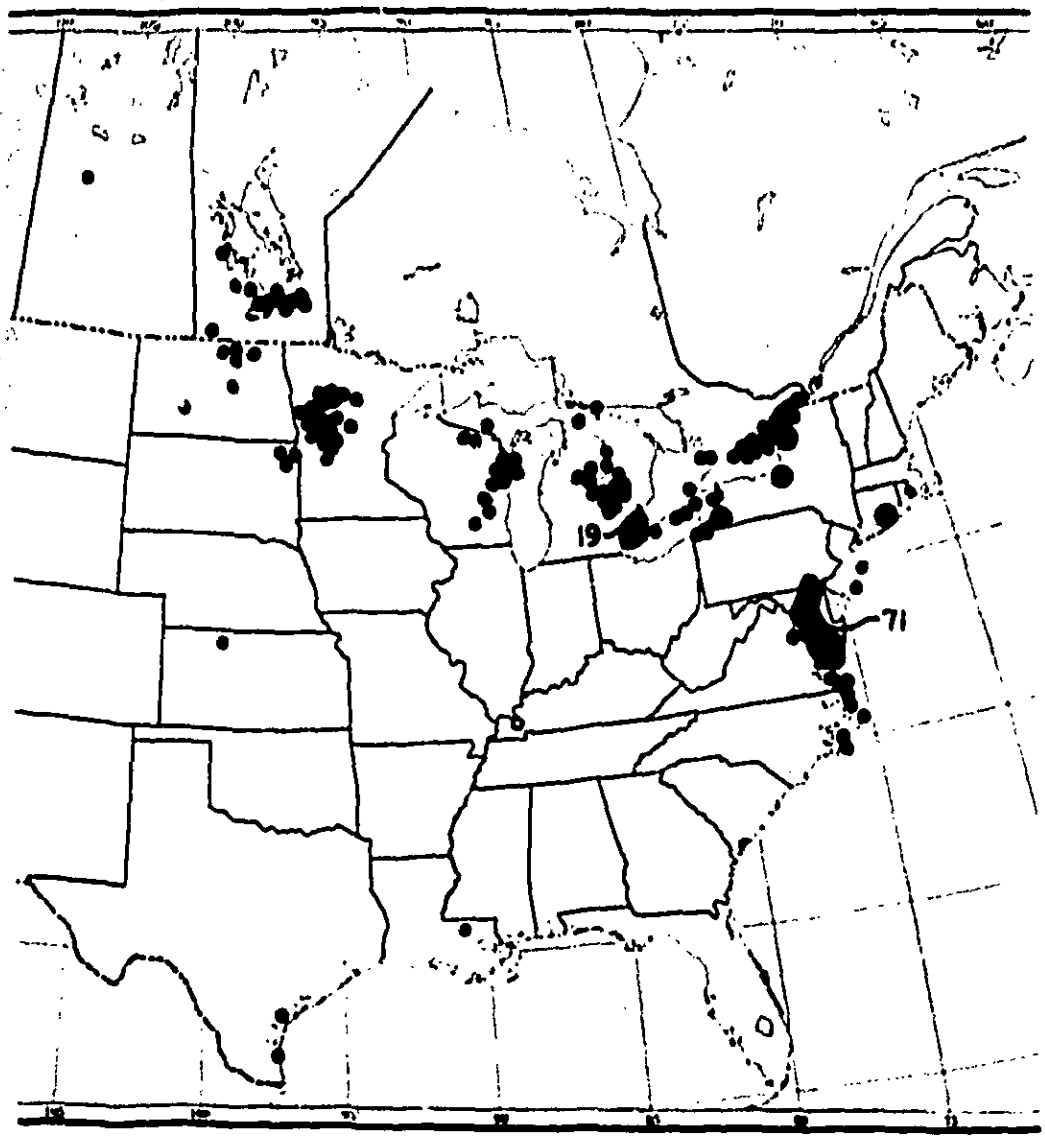

Fig. 20. Direct (fall following winter of banding) recoveries of adults banded in winter and spring at four banding stations (large dots) in New York. Numbers indicate areas where recoveries are concentrated.

route, as indicated by recoveries during and following shooting seasons. However, a small segment of *both sexes* of each group shifts to the other flyway. By recording only those band recoveries which are clearly in one flyway or the other (south of Minnesota and the Dakotas or east of Minnesota), the percentage shift has been estimated (Table 4). There appears to be more shift from west to east than vice versa, but this may be a result of greater shooting pressure along the east-

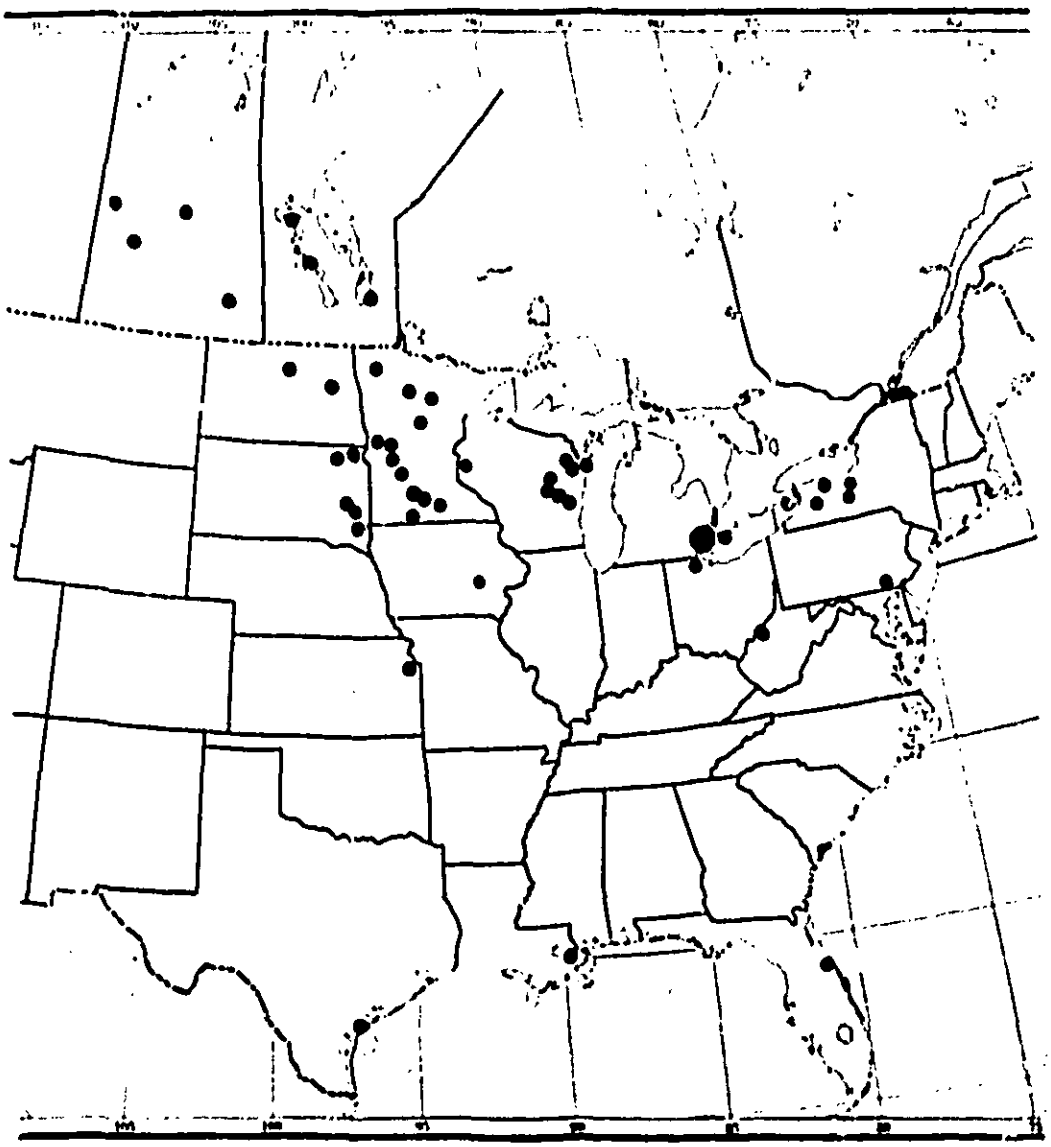

Fig. 21. Direct recoveries of adult redheads banded in winter and spring on the Detroit River, Michigan.

ern flight line. A similar eastward shift is indicated by *indirect recoveries* of birds banded as locals in most western states.

Bandings at Sand Lake in northern South Dakota indicate the complexities of an area which both southern and eastern birds pass through and where they may be banded in spring. Robbins (1919) noted that birds banded in late summer and fall were recovered equally along flight lines south and east and that indirect recoveries of spring banded birds were mainly from the south, indicating that the two groups were from different populations. Because

Table 4. Recoveries of adults banded during winter and spring in one flight line (eastward or southward) and recovered later in the other flight line

Flight	Total Recoveries	Number Shifted	Percent Shift
Eastward			
New York	146	4 (4M)	
Maryland	91	3 (3M)*	
Michigan	115	5 (3M, 2F)	
	352	12 (10M, 2F)	3
Southward			
Oklahoma	44	6	
Nebraska	70	9	
	114	15	12

* In a summary of these and later bandings, Longwell and Stotts (1958) listed 14 of 305 total recoveries (5 percent) which were later recovered in states in the Texas flight route.

of the small number of direct recoveries of locals, this theory cannot be proven yet. Any mingling of eastern and southern populations would produce a less clear-cut pattern, but shifting of birds from one flyway to another compounds the problem.

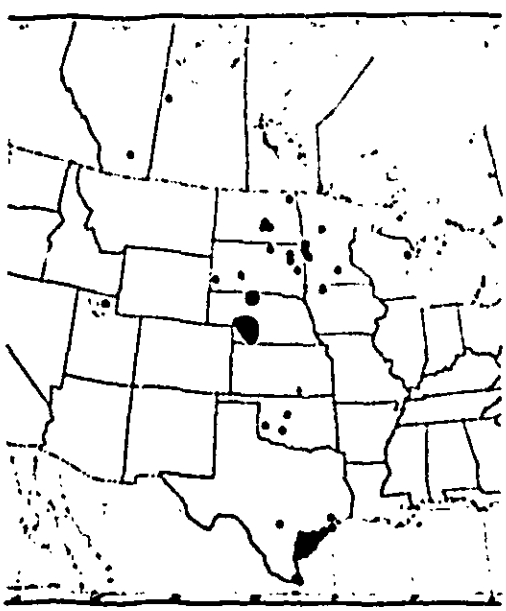

Fig. 22. Direct recoveries of adult redheads banded in Nebraska during the spring migration.

Fig. 23. Direct recoveries of adult redheads banded in Oklahoma during the spring migration.

Recoveries from spring bandings (fall bandings are rare because of hunting seasons) of adults in New York (Fig. 20) and Michigan (Fig. 21) give some insight into eastward movements of this population. Recoveries in subsequent falls show a pattern strongly indicating that, in the fall, these birds move northeastward from Michigan along Lakes Erie and Ontario. Most of them must move directly south from Lake Ontario to the Finger Lakes region, some then heading toward Chesapeake Bay, because recoveries at or north of Long Island are rare. Birds banded in New York are killed at Chesapeake Bay, while few from Michigan seem to move that far south. Recoveries from bandings in Maryland are similar to those from New York. A few birds apparently head northeastward up the St. Lawrence River and are killed in northern New York and southern Quebec. These birds presumably produce sight records common on the northeastern

coast in fall. Very few juveniles have been recovered in this northeast corner, possibly because of a more direct route south.

Banding of adults demonstrates that northward movements are not restricted to birds on the breeding areas. Recoveries of birds banded in North and South Carolina during the hunting season show northward movement into Chesapeake Bay prior to January 31. This implies either north–south shifting on the wintering areas or that birds start shifting northward soon after they reach the terminal point in their southward migration.

Chronology of Fall Migration

The time of fall migration has been estimated by ground and aerial observation, average time of band recovery, and kill data derived from hunter's bag checks.

Cooke's (1888, 1906) observers in the Mississippi Valley and in the eastern United States noted the earliest fall migrants as follows: southern Ontario, September 19; North Dakota, first week of October; Erie, Pennsylvania, October 7; Alexandria, Virginia, October 12; and Texas and Florida, early November.

Data on band recoveries are biased by opening dates of the shooting season in various north–south zones but provide large samples. Williams (1944) noted the greatest number of recoveries in October; September and November tied for second place. During these years (1929–30), hunting started in September. However, the recoveries show that, by November, most birds have left the breeding area and are killed in Texas and the southwestern tier of states. These data were supported by data from bag checks, which showed only a minor kill of redheads in the breeding area after October 31. Also, data from aerial observations on the major wintering area (the Laguna Madre) show a small redhead population in October and a major surge (if not peak) in numbers during November or December, usually maintained during January (Heit 1948, Singleton 1953).

Another system of appraising time of movement was used by Bralklage (1953) for redheads banded at Delta, Manitoba. He determined the average time of band recovery in various zones, a method also used by Weller and Ward (1959) for additional data from the same area. Based on 187 recoveries from 1938 to 1951 and 60 from 1953 (the latter figures are given in parentheses), the average recovery date for birds taken in the Dakotas and Minnesota was October 23 (October 22); the Lake states, October 24 (October 28); the East Coast, November 26 (November 30); Great Plains states, November 8 (November 14); and the Texas–Louisiana area, November 22 (December 2). Because shooting seasons during the major portion of this recovery period did not start until mid-October, no September dispersal could be measured.

Postbreeding Season Movements

Lincoln (1934) reported several unusual band recoveries (mostly indirect) from bandings at Bear River. These recoveries were taken in Michigan and on the East Coast (Figs. 15–17), suggesting that some Utah birds moved into the Atlantic as well as all other flyways. The summaries by Williams (1944) and by Robbins (1949) revealed that this flight was not nearly as significant as previously supposed. The way birds from the Great Basin reach the East Coast can probably be determined by considering the northward movements of young and adults and the behavior of adults on the breeding grounds.

First, an examination of direct recoveries of redheads banded as locals in Cali-

fornia, Utah, Nebraska, South Dakota, Minnesota, and Manitoba reveals considerable northward movement in late summer and early fall (Figs. 9–12, 14–17). Fewer recoveries are taken from bandings in northern than in southern areas, presumably because there is less shooting pressure in the far north. Indirect recoveries (adults) show a like pattern and suggest a strong eastward movement. It is, of course, impossible to know where these adults wintered, but the fact that recoveries in the east are more likely to be indirect than direct implies that an eastward shift occurred after the first breeding season.

A second line of evidence comes from recoveries of the few adults banded on breeding areas during and after the nesting period. Northward movements of less than 200 miles have been recorded for birds banded in southern Manitoba and Saskatchewan and recovered at Lake Winnipegosis in Manitoba (Fig. 19), and similar northern lakes (Cartwright and Law 1952). Still longer movements to Lake Winnipegosis are from birds banded in North Dakota. In the west, adults banded in Utah have been taken in northern Montana, and birds from Nevada have been recovered in northern California and Oregon. Hence, postbreeding movements of adults appear to be similar to the wanderings of juveniles soon after they are able to fly. To appraise these movements, it is necessary to consider observations on the biology of the redhead and other species on breeding areas.

Murdoch (1885) reported movements of eiders away from breeding areas and toward wintering areas in late summer. These movements were led by males, prior to undergoing the complete wing molt. Coombes (1950) reported movements of sheldrakes (*Tadorna tadorna*) from areas where both breeding and wintering occur. Similar behavior has been recorded for the American pochards: the canvasback and redhead (Hochbaum 1944, 1955). Flocks of these species have been observed going northward from the Delta marsh in southern Manitoba. Apparently, this movement involves both sexes, and the scarcity of adults is indicated by an analysis of hunter's bags in the Delta marsh: Hochbaum (1944) found only 8 percent adult redheads compared with 30 percent adult dabbling ducks shot in the fall. Additional data collected by Lyle K. Sowls (Personal communication, 1946 and 1947) and by the writer in 1952 and 1953 confirmed the scarcity of adults, and totaling 7 years' data produced an average figure of only 6 percent adult redheads in the fall bag. However, 14 percent were killed in 1946, and, in 1954, Nolan Perret (Personal communication) found a like percentage in the bag. This may reflect a return of birds to the marsh or a year in which more adults molted in the area. In either case, the average figure is low and demonstrates the observed exodus of adults.

Little is known of the location of *molting-lakes* or of the size of concentrations, but there are areas known for their *big northern* (= adult) redheads. In 1952, I visited shooting camps along the west shore of Lake Winnipegosis, where bands had been received from birds banded farther south during the same year. Of 251 birds checked, September 19–20, 1952, 50 percent were redheads, 55 percent of which were adults (77 percent males). Data on their weights and plumages were reported elsewhere (Weller 1957). Of 340 ducks examined there in 1953, 51 percent were redheads, over half of which were adults (75 percent males).

Because of the lack of top-caliber breeding areas nearby and the northward move-

ment of locals (indicated by recoveries). It is believed that the young-of-the-year taken at Lake Winnipegosis are mostly from more southerly and westerly breeding areas

Thus, the molt-migration of the redhead has been documented by field observations, bag checks, and limited band recovery data. Such movements partially segregate adults and juveniles and possibly sexes. Adults banded in this area have been recovered in the Delta marsh and other marshes in southern Manitoba and appear to follow the usual flight line to the eastern and southern coasts. It is also possible that mass migrations leaving the areas move southeast directly and rapidly overland, so that relatively few adults are taken in the bag in southern Manitoba.

A reasonable assumption, based on data from northward movements of both juveniles and adults, is that band recoveries taken north of a banding station demonstrate a minimal distance and that these birds could have been shot while moving southward or northward. Thus, juveniles during late summer wanderings and adults in postbreeding movements may travel due north hundreds of miles to suitable lakes, where they molt and feed. This may bring birds from even Great Basin populations northward (to summer with birds from the prairie population) and into the eastward flight lane. It could explain why more eastward than westward shift is noted among adults and might indicate that juveniles from places like Bear River move much farther north than Lincoln (1931) proposed and that they are recovered only in small numbers because of the lesser shooting pressure in the northern part of the Prairie Provinces. I do not imply that this is a major flight line but only that such movements fall within the normal behavior pattern of the species. Essentially, juveniles *explore* northern areas during their first year, producing some eastward shift of young birds reared in the west and, perhaps, experience with future molting areas. Adults moving north as molters exaggerate this shift. A reversal of this movement, from east to west, may occur during spring and fall in areas like the Dakotas and Minnesota, where southern and eastern populations mix.

SPRING MIGRATION

Little is known about spring migration, because of the scarcity of band recoveries during this season. Most recoveries of winter-banded birds occur during the fall following banding, so that two major movements occur and make any determination of routes questionable. However, if the recoveries of spring-banded birds are taken (in fall) in the same flight line in which they were banded, it is reasonable to assume that there is no major difference in spring and fall routes, at least in the area of banding and recovery. In general, this appears to be true (Figs. 22–23). However, there seems to be one example of spring-banded birds having different travel routes from fall-banded birds, but this was attributed to the presence of two slightly different populations which pass through the same area (Bobbins 1949).

There are fewer records of time of spring migration because of the lack of bag check data and of significant numbers of band recoveries. Observations by ground observers are the best data available, and Cooke's (1888, 1906) data seem as representative now as when they were gathered. These data represent average dates of arrival for first flocks of birds: Redheads reach Kansas by March 2, southeast Iowa by March 7, Nebraska and Ohio by March 10, Wisconsin and Indiana by March 13, central Iowa by March 18, southern On-

tario and southern Minnesota by March 24–30, and the northern tier of states and southern Canada by April 10–20.

SOME IMPLICATIONS OF DISTRIBUTION DATA

Area of Origin

Zoogeographers commonly use present ranges as indicators of areas of origin, assuming that species are best adapted to the locales where they evolved. When measured by density, the redhead shows preferences similar to those of its closest relative, the canvasback (Fig. 1 and Stewart et al. 1958). Because of their obvious morphological similarity and their similarity in habitat selection and behavior, these species probably did not evolve in the same geographic area. Comparing the range maps of the redhead and the canvasback, it is apparent that the redhead utilizes southerly and arid regions in the west and southwest and the canvasback uses northerly areas in Alaska and the Yukon. The implication, then, is that the canvasback developed as a northern species, whereas the redhead evolved in the alkaline water areas of the southwest. Examination of other data lends weight to this thesis:

First, 50 percent or more of the canvasback population winter in the Chesapeake Bay area whereas approximately 78 percent of the redhead population favor the Laguna Madre of Texas. Thus, the main flight route of the redhead is southward (Fig. 5); that of the canvasback is southeastward (Fig. 6). Yet, both leave the same major breeding area! For the redhead, this means a long overland flight—unusual for a species which favors lake areas. Redheads using the eastward route take the "shortest route to salt water" (Cooke 1906), but why do the majority select the longest and driest route?

Second, the redhead favors brackish water areas on its wintering ground and shows no hesitancy to rest in the ocean. Such preference (or lack of concern) by the redhead is consonant with an origin in alkaline lakes of the west, where the species still breeds in highest densities. The behavior of the two species during breeding also supports this thesis. The redhead is often considered highly social or almost colonial in nesting—a tolerance essential to species confined to limited water areas in the west. The canvasback favors small water areas where it is isolated, or occurs in low densities in large marshes where redheads are far more common. Exceptions occur, of course, but the generalization holds true for much of the range of the two species.

Third, the redhead nests late, the canvasback early (Hochbaum 1944, Weller 1959). If Baker (1938) is correct in stating that single-brooded north tropical anatids tend to nest later than do temperate species, then the later nesting season of the redhead may indicate a more southerly origin. Many factors can influence chronology of breeding season, but presumably no selective pressure toward early breeding occurs in the south, because of the long period suitable for rearing young.

Finally, the body size of the two species may suggest place of origin. If Bergmann's rule is correct, northerly species have a larger body size than do closely related, southerly species. This may hold true (for migrating birds) on wintering areas rather than breeding areas, because of lower winter temperatures (Salomonsen 1955). In any case, the larger-sized canvasback both nests and winters further north than do redheads. There are exceptions, but Bergmann's idea must be viewed from the standpoint of time of origin.

The time of isolation is unknown but

was probably associated with the great lake areas once common in the southwest and west. Just as interesting is the reason for the presumed eastward shift of redheads. This could have been an adaptation to new terrain as the original nesting area dried up, as in drought years. Or, it could have been merely a young and successful species expanding its breeding range. The type of northward movements seen today in both young and adults would make this possible. It also is apparent from viewing a map of the western mountains that any random movements of birds from Bear River or southward would take them through passes in Utah and Wyoming and bring them out in the prairies.

In any case, the species now overlap on the major portion of their ranges, and evidences of competition in breeding already are apparent (Weller 1959). The major division of the two species on the wintering areas, and probably the large size of wintering grounds, prevent serious competition for food or space in winter.

Intermixing of Populations

Mayr (1942) suggested that populations of ducks, unlike geese, mixed on the winter pairing areas and interbred, so that isolation of a gene complex was prevented. Thus, subspecies of ducks are not common on large land masses.

Such intermixing is influenced by several behavioral factors. Among redheads (and other ducks), it is known that females often home precisely to areas where they were reared or had previously nested (Weller and Ward 1959). If males did likewise, there would be a tendency toward isolation of the population, despite the fact that the pair bond in ducks is not lifelong as in geese. Present data do not clearly demonstrate homing in males: Although males are often killed, subsequently, on the area of banding, few records indicate the precise homing found in females. This may be because they select a new mate from a slightly different area of the same breeding population, or because they leave the breeding area entirely by joining a mate from another area. The available data indicate that only a small percentage of redheads shift from one flyway to another (12 percent to the east and 3 percent west); yet, this certainly adds to gene interchange. It is significant that most of the birds that shift flyways are males (Table 4). Additional intermixing could occur without being evidenced in band recovery data. For example, much mixing of populations probably occurs on postbreeding areas, where adults and young convene. Since few adults are banded on breeding areas, birds banded on postbreeding areas could represent several breeding populations. Birds from western breeding areas might join birds on more easterly wintering areas.

Another possibility of genetic interchange depends on the precise time of permanent pair formation. If pairing did not occur until birds reached Minnesota and the Dakotas, where several migration routes meet, a female from Texas could mate with a male from Chesapeake Bay. Presumably, the pair would home to the area of the female, but the male would desert her after nesting. They could then return to their respective wintering areas; the bond would go unrecorded by band recovery but genetic intermixing would have taken place.

Migration and Topography

It is common to associate major flight routes with topography, but movements of redheads follow this pattern in only a general way. Migrating redheads follow conspicuous topographic features in some

situations and avoid them in others. For example, birds reared in the northernmost and eastern portions of the range seem strongly influenced by the prairie-coniferous forest ecotone and by the chain of lakes which borders the Laurentian Shield. Superficially, it appears that a bird from any area, moving northward or eastward to this border, will move southeastward and may reach the East Coast. This movement is as much east as south. However, in the central United States, most redheads obviously move due south from the prairie region to the Laguna Madre wintering area. Over the northern portion of this route, they can move between the Rocky Mountains and the great rivers of the midwest, flying over many lakes and marshes and perhaps along conspicuous rivers like the Missouri. But in the central and southern United States, they must move predominantly across the east-west drainage pattern and over few lakes.

That this migratory pattern is set either by local topography or local bird populations is shown by experiments involving movement of hand-reared birds from the southeastward flight line (Manitoba) to the southern one (western South Dakota). These birds not only followed the migration pattern of that area but homed to it the following spring (Weller and Ward 1959).

These observations suggest that any innate directional impulse to travel southward is satisfied by a southeastward movement, as well as by one which is due south. Age may influence the degree to which birds adhere to such a flight pattern, for there are several indications that adults may traverse routes not commonly used by juveniles. For example, few juveniles seem to fly northeastward along the St. Lawrence, and fewer juveniles than adults seem to shift eastward from their original migratory routes.

The migratory pattern of the redhead does not clearly follow the classical concept of the four flyways, utilized in waterfowl management. Birds from the Great Basin-intermontane region move predominantly southward but also eastward, so that birds from the Pacific Flyway winter in the Central Flyway in east Texas. The major flight route of redheads from the prairie region is southward along the border of the Central and Mississippi flyways but clearly avoids the Mississippi Flyway. Either the flyway concept must vary for species or groups of species or our interpretations of data from these administrative units must be carefully evaluated and cautiously worded.

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